

DEMOGRAPHY AND POPULATION MODELS
FOR *HIERACIUM PILOSELLA* IN NEW ZEALAND

A thesis
submitted in partial fulfilment
of the requirements for the degree
of
Doctor of Philosophy in Plant Ecology
in the
University of Canterbury
by
S. L. Lamoureux

University of Canterbury

1998

THESIS
QK
495
.C74
.L236



Hieracium spp. in flower. Lake Ohau, Mackenzie Basin November 1996.

Table of Contents

List of Figures	iv
List of Tables	vii
Abstract	1
1. Introduction	2
1.1 <i>Hieracium pilosella</i>	2
1.1.1 History of <i>Hieracium pilosella</i> in New Zealand	2
1.1.2 Current control methods	3
1.1.2.1 Agricultural management	3
1.1.2.2 Biological control	4
1.2 Plant Population Models	6
1.3 Research Rationale	8
2. Population Dynamics and Management of a Mature Stand of <i>Hieracium pilosella</i>	10
2.1 Introduction	10
2.2 Methods	11
2.2.1 Site	11
2.2.2 Definitions	12
2.2.3 Experimental design	13
2.2.4 Statistics used in analysis	15
2.3 Results	16
2.3.1 General population dynamics	16
2.3.2 Density-dependence in <i>Hieracium pilosella</i> population dynamics	21
2.3.3 Relationships between population parameters and cover	29
2.3.4 Treatment effects on <i>Hieracium pilosella</i> population dynamics	30
2.3.5 Treatment effects on plant cover	36
2.3.6 Miscellaneous observations	38
2.4 Discussion	40
2.4.1 General population features	40
2.4.2 Density	40
2.4.3 Cover	43
2.4.4 Treatments	45
2.5 Conclusions	47

3. Age and Size distribution in <i>Hieracium pilosella</i>	49
3.1 Introduction	49
3.2 Methods	49
3.2.1 Experimental design	49
3.2.2 Statistical analysis	50
3.3 Results	50
3.4 Discussion	53
3.5 Conclusions	59
4. Soil and Site Comparison	60
4.1 Introduction	60
4.2 Methods	61
4.2.1 Site characteristics	61
4.2.2 Experimental design	62
4.2.3 Statistical analysis	64
4.3 Results	65
4.3.1 Soil analysis	65
4.3.2 Reproduction	66
4.3.3 Growth rates	70
4.4 Discussion	76
4.5 Conclusions	80
5. Modelling Population Dynamics and Biological Control of <i>Hieracium pilosella</i>	82
5.1 Introduction	82
5.2 Methods	83
5.2.1 Spatial cellular automata models	83
5.2.1.1 Starting conditions	84
5.2.1.2 Cell states	85
5.2.1.3 Daughter production and dispersal	86
5.2.1.4 Boundary conditions	89
5.2.2 Spatial coupled map lattice model	90
5.2.2.1 Starting conditions	90
5.2.2.2 Reproduction, mortality and dispersal	91
5.2.2.3 Environmental and management effects	92

5.2.2.4 Biological control	93
5.2.3 Non-spatial Ricker model	93
5.2.3.1 Biological control	94
5.2.4 Analytical spatial model	96
5.3 Results	97
5.3.1 Spatial cellular automata models	97
5.3.2 Spatial coupled map lattice model	100
5.3.2.1 Simulated dynamics of <i>Hieracium pilosella</i> at Mt John	100
5.3.2.2 Population spread	102
5.3.2.3 Effect of treatments	103
5.3.2.4 Effect of biological control	105
5.3.3 Non-spatial Ricker model	107
5.3.3.1 Simulated dynamics of <i>Hieracium pilosella</i> at Mt John	107
5.3.3.2 Effect of biological control	108
5.3.3.3 Stability analysis	111
5.3.4 Analytical spatial model	114
5.4 Discussion	114
5.4.1 Population dynamics and patch spread	114
5.4.2 Population control	117
5.4.3 Model comparison	119
5.5 Conclusions	119
6. Conclusions	122
6.1 Concluding Discussion	122
6.1.1 Context of thesis	122
6.1.2 Ecology of <i>Hieracium pilosella</i>	122
6.1.3 Population dynamics of <i>Hieracium pilosella</i> in the Mackenzie basin	123
6.1.4 Management	124
6.1.5 Implications for biological control	124
6.2 Recommendations for Further Research	125
Acknowledgements	127
References	128
Appendix 1	144

List of Figures

Figure 2.1	Timing of flower and daughter production.	18
Figure 2.2	The influx of <i>Trifolium repens</i> .	19
Figure 2.3	Effects of <i>Hieracium pilosella</i> density on mortality and population increase.	20
Figure 2.4	Daughter inflorescence initiation vs. initial <i>Hieracium pilosella</i> density.	23
Figure 2.5	Proportion of <i>Hieracium pilosella</i> rosettes producing daughters.	24
Figure 2.6	Proportion of rosettes successfully flowering.	24
Figure 2.7	The effect of <i>Hieracium pilosella</i> cover on population mortality.	27
Figure 2.8	The effect of <i>Hieracium pilosella</i> cover on daughter and stolon production.	27
Figure 2.9	The effect of <i>Hieracium pilosella</i> cover on rosette inflorescence initiation.	28
Figure 2.10	The effect of <i>Hieracium pilosella</i> cover on seedling establishment.	28
Figure 2.11	The effect of the water treatment on daughter distance and daughter inflorescence initiation.	31
Figure 2.12	Relationship of inflorescence initiation and density for fertilised and unfertilised plots.	32
Figure 2.13	The effect of water and fertiliser on <i>Hieracium pilosella</i> growth.	39
Figure 3.1	Frequency of reproduction based on the size of <i>Hieracium pilosella</i> .	51
Figure 4.1	Soil cores and <i>Hieracium pilosella</i> plants.	63
Figure 4.2	Differences in stolon length between patch position and site.	69
Figure 4.3	Relationship of final wet and dry weight for central and outside patch pairs.	75

Figure 5.1 The neighbourhoods around a focal cell.	86
Figure 5.2 Proportion of filled cells in cellular automata models for Mt. John and Wolds.	97
Figure 5.3 Wolds cellular automaton model depicting different stages in patch spread.	98
Figure 5.4 Mt. John cellular automaton model depicting different stages in patch spread.	99
Figure 5.5 Change in patch diameter with time for the Mt. John and Wolds cellular automata models.	101
Figure 5.6 Simulated population growth of <i>Hieracium pilosella</i> in the absence of any control in the coupled map lattice model.	101
Figure 5.7 The simulated rate of spread at the front in the coupled map lattice model.	102
Figure 5.8 The simulated rate of spread at the half steady-state contour in the coupled map lattice model.	103
Figure 5.9 The simulated effect of fertiliser and fertiliser + water on density.	104
Figure 5.10 The simulated effect of a biological control agent on <i>Hieracium pilosella</i> .	106
Figure 5.11 Simulated long-term suppression of a population of <i>Hieracium pilosella</i> under different levels of biological control.	107
Figure 5.12 Simulated population growth from the Ricker model.	108
Figure 5.13 The simulated effect of increasing mortality in a Ricker model.	109
Figure 5.14 The effect of reducing the number of daughters per rosette in a stable population of <i>Hieracium pilosella</i> .	110
Figure 5.15 The simulated effect of biological control in the form of increased mortality on the total cover of <i>Hieracium pilosella</i> from the Ricker model.	110

Figure 5.16 The simulated effect of biological control in the form of decreased daughter production on the total cover of *Hieracium pilosella* from the Ricker model.

List of Tables

Table 2.1 Mean monthly and annual temperature and rainfall data for Lake Tekapo.	12
Table 2.2 ANCOVA and regression equation for the proportion of <i>Hieracium pilosella</i> rosettes and daughters dying.	21
Table 2.3 ANCOVA and regression equation for the proportion of non-reproductive <i>Hieracium pilosella</i> rosettes and daughters dying.	21
Table 2.4 ANCOVA and regression equation for <i>Hieracium pilosella</i> seedlings per rosette.	22
Table 2.5 ANCOVA and regression equation for population change of <i>Hieracium pilosella</i> .	22
Table 2.6 ANCOVA and regression equation for <i>Hieracium pilosella</i> daughter rosette inflorescence initiation.	23
Table 2.7 ANCOVA and regression equations for the effect of % <i>Hieracium pilosella</i> cover on various demographic parameters.	25
Table 2.8 <i>Hieracium pilosella</i> demographic parameters which were found to have no association with % cover of other species.	29
Table 2.9 Treatment means and <i>p</i> -values for the effect of four environmental treatments on various demographic parameters in <i>Hieracium pilosella</i> .	33
Table 2.10 Means for the two-way interaction between fertiliser and water.	34
Table 2.11 Means for the two-way interaction of fertiliser and cutting.	35
Table 2.12 Mean seedlings per rosette for the three-way interaction between water, fertiliser and cutting.	35
Table 2.13 Means for the average cover of <i>Hieracium pilosella</i> and <i>Trifolium repens</i> under the main treatment effects.	36
Table 2.14 Means for the two-way interaction of fertiliser and cutting on the cover of <i>Hieracium pilosella</i> and <i>Trifolium repens</i> .	36

Table 2.15 Means for the three-way interaction between water, fertiliser and cutting on the cover of <i>Hieracium pilosella</i> and <i>Trifolium repens</i> .	37
Table 2.16 ANCOVA and regression equation for the relationship between <i>Hieracium pilosella</i> and <i>Trifolium repens</i> cover (%).	38
Table 3.1 ANOVAs of size and reproduction for <i>Hieracium pilosella</i> .	52
Table 3.2 Reproductive <i>Hieracium pilosella</i> rosettes in two age groups.	52
Table 3.3 Mean nearest neighbour distance for reproductive and non-reproductive <i>Hieracium pilosella</i> rosettes.	52
Table 3.4 Percentage of <i>Hieracium pilosella</i> rosettes initiating inflorescences by age and size.	53
Table 3.5 Mean longest leaf length and diameter for <i>Hieracium pilosella</i> rosettes in two age classes.	53
Table 3.6 Some facultative biennial plant species where size thresholds for reproduction have been shown.	55
Table 4.1 Means from soil analyses for soil cores from within and outside of <i>Hieracium pilosella</i> patches at two sites.	66
Table 4.2 Percent of rosettes initiating inflorescence and treatment means for other reproductive attributes for <i>Hieracium pilosella</i> in soil cores from within and outside Mt. John and Port Levy <i>H. pilosella</i> patches.	67
Table 4.3 General Linear Model for the reproductive attributes of <i>Hieracium pilosella</i> grown in soil cores from within and outside Mt. John and Port Levy <i>H. pilosella</i> patches.	68
Table 4.4 Backwards step-wise multiple regression of <i>Hieracium pilosella</i> inflorescence initiation and daughter production vs. soil nutrients, pH or soluble aluminium.	69

Table 4.5 Means for weight ratios of <i>Hieracium pilosella</i> grown in soil cores from within and outside Mt. John and Port Levy <i>H. pilosella</i> patches.	70
Table 4.6 General Linear Model for final:initial weight ratios of <i>Hieracium pilosella</i> grown in soil cores from within and outside Mt. John and Port Levy <i>H. pilosella</i> patches.	71
Table 4.7 Mean dry weights for <i>Hieracium pilosella</i> plants grown in soil cores from within and outside Mt. John and Port Levy <i>H. pilosella</i> patches.	73
Table 4.8 General Linear Model for dry weight of <i>Hieracium pilosella</i> grown in soil cores from within and outside Mt. John and Port Levy <i>H. pilosella</i> patches.	73
Table 4.9 General Linear Model for root:shoot ratio of <i>Hieracium pilosella</i> grown in soil cores from within and outside Mt. John and Port Levy <i>H. pilosella</i> patches.	74
Table 4.10 Backwards step-wise multiple regression of <i>Hieracium pilosella</i> weight ratios and soil nutrient content.	75
Table 4.11 Summary of results for various differences between soil cores taken from <i>Hieracium pilosella</i> patch centres and areas outside of patches at Mt. John and Port Levy.	77
Table 5.1 Reproductive, survival and dispersal parameters used in the cellular automata models.	88
Table 5.2 Reproductive rates and mortality equations used in the coupled map lattice model.	92
Table 5.3 Mean non-reproductive mortality for <i>Hieracium pilosella</i> under the two-way interaction of water and fertiliser.	104

Abstract

Hieracium pilosella has become a major concern in the high country grasslands of New Zealand. This thesis provides an understanding of the population dynamics of *H. pilosella* in an area which has supported the weed as a major component of the vegetation for more than 30 years. The study uses a combined modelling and experimental approach to determine vital rates and regulatory mechanisms. It then uses these to predict the rate of spatial spread, change in density, and the likely impact of biological control.

Mature populations of *H. pilosella* at Mt. John were found to be regulated by the interaction between density-dependent mortality and density-independent reproduction. The addition of water and/or fertiliser caused an increase in the reproductive vigour of the plant and a decrease in density while simulated grazing (i.e. mowing) had little effect on the population. A link was found between reproductive vigour and rosette size or age (50% of first year rosettes reproduced while only 11% of older rosettes did), although the reproductive threshold size (23 mm diameter) appeared to be independent of age. Rosettes grown on soil which had previously supported *H. pilosella* had lower growth and reproductive rates and produced fewer stolons of shorter length. However, there was little support for either the allelopathic or aluminium toxicity hypotheses for these lower growth rates.

Spatial population models suggested that in the early stages of colonisation, *H. pilosella* vital rates are such that it has the potential to occupy 100% of available space but as the population matures, vital rates change and it is unable to occupy all available space, probably because of intraspecific competition and a limit on plant size. Spread of patches was predicted to be 0.5 - 0.8 cm/yr by both explicit spatial simulation models and analytical diffusion models. Both spatial and non-spatial models predicted that the most effective agent for biological control would be one which caused an increase in mortality rather than a decrease in fecundity; to reduce a population by more than 50% a control agent would have to either increase mortality by 10 - 15 % or decrease daughter production by 80%.

1. Introduction

1.1 *Hieracium pilosella*

1.1.1 History of *Hieracium pilosella* in New Zealand

There are presently 9 species of hawkweed which occur in New Zealand. Of these, four are considered to be problem weeds in New Zealand grasslands: *Hieracium pilosella* L. (mouse-ear hawkweed); *H. praealtum* Gochnat (king devil hawkweed); *H. caespitosum* Dumort. (field hawkweed); and *H. lepidulum* (Stenstrom) Omang (tussock hawkweed) (Webb, Sykes & Garnock-Jones 1988).

H. pilosella is the most problematic hawkweed species in the grasslands of New Zealand. It occurs in drier areas from Marlborough to Southland in the South Island and in central and eastern parts of the North Island (Webb *et al.* 1988; Hunter 1991). In the South Island high-country, it is most abundant in a rainfall range of 600 - 1200 mm and below 1000 m but can be found at altitudes of up to 1700 m (Hunter 1991).

It was first recorded in New Zealand in 1878 and is thought to have arrived from Europe in impure pasture seed (Anonymous 1976). From 1920 to 1963, *H. pilosella* continued to spread but was still a rare species (Allan 1920 & 1940; Kerr 1950; Barker 1953; Moore 1955 & 1976; Connor 1964). By 1974, *H. pilosella* was a common species in the Mackenzie Country and Molesworth Station with cover of more than 90% in localised areas (Stevens & Hughes 1973; Moore 1976; Makepeace 1980).

There has been a general debate as to whether *H. pilosella* is the symptom or cause of land degradation in the New Zealand high country (Hunter 1991; Hunter, Mason & Robertson 1992). Treskonova (1991a & 1991b) suggested that the expansion of *H. pilosella* in the high-country was due to the gradual degradation of land under pastoral systems while Scott (1985 & 1993b) took the view that *H. pilosella* was an aggressive invader well adapted to the low-fertility tussock grassland environment.

H. pilosella is a prostrate stoloniferous species which produces dense mats that exclude both pasture and native species and has the ability to colonise open or vegetated areas. These growth habits make it a major concern for both economic and environmental reasons. *H. pilosella*'s ability to exclude other species has resulted in a dramatic decrease

in pasture and native species in some high-country areas. The reduction in pasture species has caused a decrease in productivity of up to 30% (South Island High Country Review Committee 1994 cited in Espie 1994). It has been shown that sheep preferentially graze *H. pilosella* but have a limited ability to feed on it because of its prostrate habit (Hughes 1975; Scott 1985; Jenkins 1992).

The general population ecology of *H. pilosella* has been summarised by Bishop and Davy (1994). Scott (1985) and Jenkins (1992) reviewed the characteristics of populations in the New Zealand environment. *H. pilosella* is a monocarpic perennial herb which reproduces both sexually and vegetatively. While initial establishment in New Zealand would have been by seed, its spread is mostly vegetative through the production of stoloniferous or axillary daughter rosettes (Makepeace 1985a; Jenkins 1995). Flowering and stolon production are closely linked, with stolon production occurring only after inflorescence initiation. Reduced inflorescence production has been observed in high-density populations and in the central region of patches (Makepeace 1985a), and appears to be due to limited nutrient availability (Davy & Bishop 1984). Allelopathic activity by *H. pilosella* has been suggested (Widera 1978; Makepeace, Dobson & Scott 1985) but there has been no conclusive proof of an allelopathic effect in the field (Makepeace *et al.* 1985; Henn, Petit & Vernet 1988). A more detailed account of the population dynamics of *H. pilosella* will be reviewed within the appropriate chapters.

1.1.2 Current control methods

1.1.2.1 Agricultural management

Scott, Robertson and Archie (1990a) found that appropriate grazing management, sowing of pasture species and application of fertiliser can suppress *H. pilosella* in New Zealand. They showed that, under little or no fertiliser inputs, *H. pilosella* was able to remain the dominant species while under high fertiliser application combined with the sowing of legumes *H. pilosella* became rare within 2 - 6 years. Similarly, in a 9 year trial at Mt. John, Lake Tekapo, Scott (1993a) showed that *H. pilosella* decreased or disappeared under high fertiliser input and sowing of pasture species, particularly with the addition of irrigation.

Grazing has also been suggested as a strategy for slowing the spread of *H. pilosella* on low-input land by reducing flowering and hence, seedling establishment (Espie 1994). Grazing intensity may also affect *H. pilosella* cover. Espie (1994) suggested that maintaining lower stocking rates allowed for an accumulation of standing herbage possibly resulting in lower *H. pilosella* cover. However, in a pasture improvement trial, Scott *et al.* (1990a) found that the effect of different grazing intensities on *Hieracium* abundance was minor.

1.1.2.2 Biological control

The control of hawkweeds using herbicides or oversowing and topdressing with fertiliser is often not practical, because these methods are either uneconomical or inappropriate for areas in which *H. pilosella* is a problem. An alternative approach is biological control using insects and/or fungi.

Rusts have the ability to sporulate rapidly and prolifically, can disperse efficiently and can be highly host-specific. These attributes, along with their ability to cause disease epidemics, make them excellent candidates for biological control agents (Evans & Ellison 1990). Thus, the rust *Puccinia hieracii* var. *piloselloidarum* was studied in Europe as a potential biological control agent for the control of *H. pilosella* in New Zealand (Jenkins 1995; Morin & Syrett 1996). In April 1995, it was unexpectedly found already to occur within New Zealand. Jenkins (1995) determined that the rust was not a threat to non-target plants in New Zealand because of its limited host-range. In their pilot study, Morin and Syrett (1996) found that plants grown from 14 different New Zealand seed collections responded differently to rust isolates from Pitlochry, Scotland and Lincoln, New Zealand. In the same study, Morin and Syrett found that plants from five of the fourteen seed collections did not develop any uredinia (indicating a resistance to the rust) when the Pitlochry isolate was used. Of the remaining nine, four had less than 10% of the total inoculated plants developing uredinia (susceptible response), four had between 20% and 50% developing uredinia, and only one had more than 50% of the plants developing uredinia with the Pitlochry isolate. Plants inoculated with the New Zealand isolate showed an overall higher proportion of plants developing uredinia. Only one site showed a resistance to the New Zealand isolate and two sites had 100% of the plants developing uredinia. The site which had no response to the New Zealand isolate

also gave no response to the Pitlochry isolate. This difference in response to the rust isolates by plants from different populations of *H. pilosella* may indicate genetic variation in susceptibility throughout New Zealand (Jenkins 1995; Morin & Syrett 1996).

Insects are also being considered for *Hieracium* control in New Zealand. There was no evidence of insects within New Zealand likely to have a significant impact on *Hieracium* populations so a study was carried out in Europe to seek suitable insect control agents for introduction into New Zealand. Host-specificity tests have begun on four species: a pterophorid moth, *Oxyptilus pilosellae*; a cynipid wasp, *Aulacidea subterminalis*; a gall midge, *Macrolabis pilosellae*; and a syrphid, *Cheilosia praecox* (Syrett *et al.* 1996).

Oxyptilus pilosellae

The larvae of this moth feed in the rosette centre, on leaves and root crowns of both parent and daughter rosettes. The species is strictly monophagous, recorded exclusively from *H. pilosella* (Syrett *et al.* 1996). It was introduced into quarantine in New Zealand in November 1996 (P. Syrett, *pers. comm.*).

Aulacidea subterminalis

This is a gall wasp which reproduces parthenogenetically. Eggs are laid into stolon tips and the larvae induce large swollen galls at the base of the *Hieracium* rosettes. Infested rosettes were observed to be heavily deformed by late summer (Syrett *et al.* 1996). This species is also restricted to *H. pilosella* and was introduced into quarantine in New Zealand in 1997 (P. Syrett, *pers. comm.*).

Macrolabis pilosellae

This gall midge deforms developing stolons and rosettes and the leaves become tightly curled and do not unfold (Syrett *et al.* 1996). It is restricted to *Hieracium* spp. and will be introduced into quarantine in New Zealand in 1998 (P. Syrett, *pers. comm.*).

Cheilosia praecox

The larvae of this syrphid feed on young leaves, rosette centres and root crowns. It is not clear whether this species is restricted to *H. pilosella* or if it feeds on other

Hieracium spp (Syrett *et al.* 1996). Introduction to quarantine in New Zealand is planned for 1998 (P. Syrett, *pers. comm.*).

Tests on the impact of effective biological control on ground cover are being carried out, by artificially removing *Hieracium* from small plots to discover which plants, if any, will replace the *Hieracium* rosettes. Initial findings are that total indigenous vegetation, total exotic vegetation (excluding *Hieracium*), litter, and bare ground have all increased in the treated plots (Syrett *et al.* 1996).

1.2 Plant Population Models

Studies in plant population ecology began early in the twentieth century, with an emphasis on community classification. Early plant models in the 1960s focused on crop yields or functions of seed density (Silvertown 1987) and selective logging techniques in forests (for example Usher 1966, 1969a & 1969b). Later in the 1970s, plant ecologists began adapting the population projection matrix model of Leslie (1945 & 1948) to populations with complex life cycles (Sarukhán & Gadgil 1974; Hartshorn 1975; Werner & Caswell 1977; Caswell & Werner 1978; Enright & Ogden 1979 to name a few). In 1980 one of the first logistic-type models was developed for a plant population (Watkinson 1980) and was subsequently extended to include a seed bank (MacDonald & Watkinson 1981).

Given that the earliest population theory focused on animals (Lotka 1925 and Volterra 1926 cited in Harper 1977; Leslie 1945 & 1948) and that the vast majority of theory still does, plant ecologists have relied heavily on theory developed by animal ecologists. While this animal based theory was initially useful, during the 1980s there was a call for plant ecologists to develop more appropriate theory which included the fundamental characteristics of plants: autotrophy, sedentary habit, spatially local interactions, plastic growth, and clonal habit (Antonovics & Levin 1980; Weiner & Conte 1981; Crawley 1986; Pacala 1989).

Since the early 1980s, the modelling of plant populations has increased greatly. The use of matrices has increased (see Caswell 1989 for a review) and Mack and Harper (1977) developed a model which emphasised the neighbourhood structure of plant populations.

Neighbourhood models were further refined by Weiner (1982) and Pacala and Silander in several papers (Pacala & Silander 1985 & 1990; Pacala 1986a, 1986b & 1987) and continuous diffusion models were developed by Hara and others (Hara 1986, 1988 & 1993; Hara, Van der Toorn & Mook 1993). In addition, the field of cellular automata and metapopulation theory (coupled map lattice models), in describing the spread of both plant and animal populations through time, is now expanding. Cellular automata models have been used to look at species interactions (Crawley & May 1987) and the effect of immigration among local populations (Hassell, Comins & May 1991) as well as disturbance on community structure (Green 1989), and have gained increasing popularity in plant ecology (Barkham & Hance 1982; van Tongeren & Prentice 1986; Crawley & May 1987; Hobbs & Hobbs 1987). The use of coupled map lattice models in plant ecology is less common (Hobbs & Hobbs 1987; Kadmon & Shmida 1990; Tilman 1994).

Spatial models in plant population ecology are of special interest: because plants are sessile, the amount of competition on any individual is dependent on the proximity of its neighbours. Simple cellular automata and coupled map lattice models can be used to examine the spatial structure of populations as well as their spread through time. In addition they are useful in determining the effect a biological control agent will have on the population's distribution and ability to spread to new areas.

The modelling of biological control in weed populations is still in its infancy. Most biological control models to date have dealt with host/parasitoid systems. In a recent review of biological control models, Barlow (in press) found that in all of the plant models reviewed, none modelled the population dynamics of the control agent; biological control was introduced into the model either as additional mortality or as reduced fecundity. In this sense, most of these models give only part of the story. They are, however, useful in determining characteristics of a control agent which will give the best results and whether a realistically attainable effect on the plant's vital rates can significantly suppress its density.

A more general benefit of models is their ability to help refine and target research questions. This can help shorten the time required for population studies, which is

particularly valuable given the current trend away from long-term studies to those lasting 5 years or less.

1.3 Research Rationale

The ultimate aim of this study was to develop population models of *Hieracium pilosella* which would explain population dynamics, predict spatial spread at a population level and allow us to predict the likely impact of the biological control agents currently being studied.

The past two decades have shown a marked increase in research into the *Hieracium* problem in New Zealand. Of the dozens of studies carried out on this plant, only one has attempted to explain aspects of the population dynamics of this weed at the rosette level (Makepeace 1980). The other studies have focused on population or community-level measures such as cover or frequency (Scott *et al.* 1990a & 1990b; Treskonova 1991a; MAF 1992, 1993, 1994 & 1995; Scott & Sutherland 1993; Espie 1994; Rose, Platt & Frampton 1995). Makepeace provides valuable information on the dynamics of *Hieracium* in the colonising and expanding phases of invasion but gives very little information on mature populations. Also, data collected by Makepeace did not provide an indication of non-reproductive mortality, particularly over the winter period. Hence, an understanding of the dynamics of a mature stand of *H. pilosella* was required before population models could be developed that accurately predict population dynamics through time.

This study has expanded our existing knowledge of *H. pilosella* population dynamics by studying the growth and reproduction biology over 1 to 2 years of a mature population under different environmental conditions. Population models were then developed to predict the plant's ability to colonise and spread and the likely impact of biological control. In Chapter 2, population dynamics of a mature population of *H. pilosella* situated at Mt. John, Lake Tekapo, New Zealand are described, including the effects of environment and density or cover on birth and death rates. Chapters 3 and 4 further explore the demography of *H. pilosella*. In Chapter 3, the effect of age and size on reproductive rates are assessed while Chapter 4 explores the relationship between the history of *H. pilosella* on soils and rosette size or reproductive ability. Finally, Chapter 5

examines the population dynamics and spatial spread of *H. pilosella* by way of spatial and non-spatial models and explores the effect of various forms of biological control on the population.

2. Population Dynamics and Management of a Mature Stand of *Hieracium pilosella*

2.1 Introduction

There have been several studies of *Hieracium pilosella* in New Zealand but most have focused on the change in rank, cover or frequency of populations over time (Scott *et al.* 1990a & 1990b; Treskonova 1991a; MAF 1992, 1993, 1994 & 1995; Scott & Sutherland 1993; Espie 1994; Rose *et al.* 1995). While studies which look at general trends over time are useful, they do little to help explain the reasons underlying these changes. There have been three other field studies of the population dynamics of *H. pilosella* at the plant level; two overseas studies in Britain and Poland (Bishop, Davy & Jefferies 1978; Widera 1978; Bishop & Davy 1984) and one study within the New Zealand environment (Makepeace 1985a). With the exception of his Sawdon site, Makepeace's sites consisted of populations which were in a colonising state. It was hoped that a study in an area in which *H. pilosella* has been the dominant component of the plant community for 3 or more decades could provide information on the population dynamics of a mature or over-mature stand. This information, combined with Makepeace's demographic data from the colonising phase, could then be combined within a population model to help explain the spread of populations and possibly give predictions for the future of land in which *H. pilosella* has become a major concern.

The response of plants to fertiliser, moisture and defoliation is important in understanding the overall dynamics of a population. Several authors have looked at the change in cover or rank of *H. pilosella* with the addition of fertiliser (Hay & Ouellette 1959; Scott *et al.* 1990a; Scott 1993a; Svavarsdóttir 1995). In all cases there was a general decrease in the cover of *H. pilosella* populations, probably due to intraspecific or interspecific competition. None of these studies related the addition of fertiliser to changes in the demography of the population. Two experiments addressed the effect of fertiliser in glasshouse pot trials (Makepeace 1985b; Svavarsdóttir 1995). In both, the response of *H. pilosella* to added nitrogen and phosphorus resulted in an increase in stolon production. Only one study has considered the effect of nutrient addition on the population dynamics of *H. pilosella* in the field (Davy & Bishop 1984). This showed an increase in the proportion of rosettes initiating capitula and stolons.

The aim of this field experiment was to quantify the demographic parameters in a mature stand of *H. pilosella*, at Mt. John, Lake Tekapo, under different environmental conditions. The site has had high densities of *H. pilosella* since the 1960s and consists mainly of *H. pilosella* and bare ground. The first part of this chapter describes the effect of intraspecific density and cover on the population dynamics of a mature stand of *H. pilosella*. The second part of the chapter looks at changes in reproduction and mortality under four different treatments (fertiliser, water, clipping and insecticide/fungicide).

2.2 Methods

2.2.1 Site

The experiment took place at AgResearch's Mt. John Trial Site (43° 59'S, 170°27'E, elevation 820 m) during the 1994-96 growing seasons. The mean yearly temperature at the Lake Tekapo meteorological station for the study period was 8.1°C and the average yearly rainfall was 763.5 mm. The temperature was slightly lower than the 70-year average of 8.8°C while the mean rainfall was 26% higher than the 70-year average of 605 mm (New Zealand Meteorological Service). Monthly averages are shown in Table 2.1. In the first year of the study, 1994, when most of the demographic data were collected, rainfall was dramatically higher during September and November than the 70-year average, although the total for the three spring months of September - November was average. Summer rainfall for December 1994 to February 1995 was lower than the average. There were no extreme departures from average temperatures during the first year although the spring temperatures were below average while the summer temperatures were slightly above. During the second year of the study, rainfall for September, December and April were well above average. The month of July, 1995, had average temperatures well below normal and the spring temperatures were slightly cooler than average.

The Mt. John Trial Site was modified short tussock grassland prior to the commencement of agricultural trials in 1982 and had no previous history of fertilisation or sowing of agricultural species. The area had visual estimates of 70 - 80% *Hieracium pilosella* cover (D. Scott, *pers. comm.*). Other species which occurred consistently in the area in approximate order of abundance were *Festuca novae-zelandia*, *Erythranera pumila*,

Cyathodes fraseri, *Pimelea oreophila*, *Wahlenbergia albomarginata*, *Coprosma petriei* and *Trifolium repens*. The 0.25 ha plot used for this study was still in the above state when this study commenced in October 1994.

Table 2.1 Mean monthly and annual temperature and rainfall data for Lake Tekapo. 70-year averages cover the period 1927 - 1996. Data from New Zealand Meteorological Service, Lake Tekapo station.

	Rainfall (mm)			Average Temperature (°C)		
	70-Year	1994/95	1995/96	70-Year	1994/95	1995/96
May	54.2	54	39	5.8	5.7	7.2
June	53.6	70	77	2.6	1.8	2.5
July	48.9	74	33	1.5	2.1	-2.7
August	53.6	72	57	3.4	4.2	1.9
September	53.1	111	122	6.6	4.3	4.8
October	53.8	17	58	9.2	7.6	8.3
November	47.0	125	48	11.2	9.8	10.1
December	52.2	5	125	13.5	13.7	14.0
January	48.1	15	19	14.9	15.2	15.2
February	40.1	28	54	14.8	15.9	13.6
March	49.1	85	38	12.7	12.0	10.4
April	51.6	73	128	9.5	9.1	8.2
Annual	605.1	729	798	8.8	8.5	7.8

The trial site was fenced to exclude rabbits, and periodic poisoning within the site was carried out to limit the effect of rabbits which may have entered. During the period of this study, there was no evidence of rabbit activity although there was the remnant of a latrine at one of the plots. The site had been grazed by sheep prior to 1982 and was lightly grazed only twice between 1982 and the commencement of this study.

2.2.2 Definitions

With clonal species it is difficult to delineate individual plants. For simplicity, this study will follow the definitions given by Makepeace (1980). Rosettes are defined as individuals distinctly connected to the soil by roots. Progeny produced vegetatively and not from seed are referred to as daughters. Those daughters which occurred in the same place as the parent rosette and had no discernible stolon are referred to as axillary daughters while those occurring on the end of a definite stolon are called stoloniferous daughters.

H. pilosella is known to produce seed both asexually and sexually. These two forms of seed production were not distinguished in this study, so all individuals derived from seed will be referred to as seedlings.

2.2.3 Experimental design

The environmental experiment had a factorial design with the following treatments commencing in October 1994:

Fertiliser (2 levels)

Nil or $0.1 \text{ kg m}^{-2} \text{ yr}^{-1}$ slow release Osmocote fertiliser which contained 15% nitrogen, 3.5% phosphorus, and 9.1% potassium. Applied October 1994 and October 1995.

Simulated grazing (2 levels)

Nil or monthly cut to 1-2 cm in height to remove flower and seed heads and tall leaf material.

Moisture (2 levels)

Nil or mist spray fortnightly for 12 hours (approximately 80 mm of water), from December to March, to maintain soil moisture levels and to encourage seedling establishment.

Fungicide + Insecticide (2 levels)

Nil or monthly spraying with a systemic fungicide, Topaz MZ, and general insecticide, Septan, to establish a control for further tests with biological control agents.

Spatial replication (2)

The study site consisted of 32 $1.2 \times 1.2 \text{ m}$ plots, each surrounded by a 4 m buffer area to allow for independence between treatment combinations. The plots were laid out in columns with treatments applied in a non-random manner (Appendix 1). While this was not ideal it was historical. Each plot was subdivided into 40 $14 \times 24 \text{ cm}$ subplots. Plot and subplot boundaries were defined by permanently fixed wire grids. Plot and subplot

size were determined by the fixed dimensions of the wire grid used while quadrat size was chosen for ease of mapping plants at high densities.

A 7×7 cm quadrat was placed in 3 - 10 of the subplots. The boundaries of these quadrats were also defined with the use of permanently fixed wires (see treatment map, appendix 1). For statistical purposes a minimum of 100 rosettes per plot were initially mapped. To achieve this, quadrat corners were located randomly in each of the randomly selected subplots until a total of approximately 100 rosettes were mapped for each plot.

All rosettes, daughters and stolons in each of the 7×7 cm quadrats were mapped onto graph paper during December 1994 so that each could be accurately relocated during subsequent visits. Bud, flower and stolon initiation and growth, daughter production and general appearance were recorded for each rosette at each visit. In addition, the death of rosettes, the establishment and death of seedlings and daughters, and any other notable features were recorded.

For each rosette which reproduced, the number of stolons, stolon length and daughter distance were measured. Stolon length was measured along the stolon from the rosette's centre to the end of the stolon whereas daughter distance was measured as a straight line from rosette centre to daughter centre.

The plots were visited five times during the 1994/95 growing season to follow the main life history stages and three times during the 1995/96 growing season to record winter survival and to obtain relative changes in density:

Oct. 1994 - to record initial population densities and early flower or stolon production;

Dec. 1994 - to record flower production;

Jan. 1995 - to record seed and stolon production and flower abortion;

Feb. 1995 - to record daughter rosette production and seedling germination;

Apr. 1995 - to record daughter and seedling establishment and death;

Oct. 1995 - to record over-winter survival;

Dec. 1995 - to record rosette and daughter density;

Apr. 1996 - to record end of season rosette density.

Only the control and fungicide plots were followed for the second year (from October 1995) because a dramatic increase of growth in the fertilised and watered plots during the first year made it impossible to accurately locate individually mapped rosettes.

In addition to the above sampling, vertical photographs of each of the quadrats were taken in February 1995 and February 1996. Visual estimates for *H. pilosella* and bare ground cover were obtained from the photographs by two independent observers. Those plots where cover estimates were notably different between the two observers were re-examined and the cover estimate was decided by consensus. Cover was recorded using 5% cover classes with two additional classes of 1% and 99%. The 1% class was used when cover was slightly greater than 0% and the 99% class was used when the cover was slightly less than 100%. Cover estimates were also made for *Trifolium repens* using the February 1996 photographs.

2.2.4 Statistics used in analysis

The demographic data were analysed using Genstat 5 (Genstat 5 Committee 1993). ANCOVAs were used to analyse the effect of initial rosette density or percent *H. pilosella* cover on population attributes such as daughter production, flower initiation and success, seedling recruitment, per capita rate of change, stolon production and daughter distance with plots as a factor. Mortality was analysed in the same way with the exception that total density (rosettes + daughters) was used instead of initial rosette density. Total density was used because separate mortality rates for daughters and rosettes were not available owing to the problems encountered in relocating mapped individuals later in the season. While quadrats within plots cannot be considered independent for analysis of treatment effects they can be used to determine relationships between variables within plots (D. Saville, *pers. comm.*; Saville & Wood 1991). This was achieved by using the plots as the factor in the analysis allowing the variation within plots to be accounted for (Saville & Wood 1991). This method also adjusts the plot means to single, overall means so that treatment effects can be analysed using these overall means rather than individual means. These adjusted plot means from the

ANCOVA for each dependent variable were subsequently analysed for treatment effects by using an ANOVA with combinations of the treatments as factors.

Regression lines were fitted to data using the methods describe in Saville and Wood (1991):

$$(y - \bar{y}) = \beta(x - \bar{x})$$

where \bar{y} is the mean dependent variable, \bar{x} is the mean of the covariate (independent variable), and β is the fitted slope from the ANCOVA. In all ANCOVA tables, a significant covariate F-value denotes a regression slope significantly different from 0.

To deal with the non-randomness in treatment application, the plot residuals from the treatment ANOVAs were separately regressed against rows and columns (D. Saville, *pers. com.*). In doing this, the effects of the treatments are removed leaving any remaining effects. When this was done, there were very few row or column (i.e. position) effects on any measured plant performance variable (e.g. stolon and daughter production, mortality, inflorescence initiation and abortion, etc.). Therefore, it was assumed that row and column effects had little effect on plant performance and were not responsible for the other effects found.

Because quadrats were randomly selected within the plots it can be assumed that the average initial cover was equivalent between plots, hence, average cover of clover (*Trifolium repens*) and *H. pilosella* estimated from the second set of photographs were analysed for treatment effects by using an analysis of variance assuming equal means.

2.3 Results

2.3.1 General population dynamics

A total of 3343 rosettes, 878 daughters and 35 seedlings were followed within 214 quadrats during the 1994/95 growing season. Inflorescence initiation began in October, with flowering continuing until April. Peak flowering occurred between December and January (Figure 2.1). 682 rosettes (20%) and 108 daughters (12%) initiated inflorescences of which 43% and 36% respectively aborted before successfully seeding. In 13% of rosettes which initiated inflorescences, it appeared as though individual

rosettes produced more than one inflorescence. In most cases the buds occurred sequentially with the second bud occurring before the first had fully developed into an inflorescence. Because *Hieracium pilosella* is reported as being monocarpic and produces a single inflorescence (Bishop & Davy 1984; Bishop & Davy 1985; Makepeace 1985a; Bishop & Davy 1994), it was assumed that these rosettes had initiated an axillary daughter rosette which began to flower before it was able to develop its own leaves. This follows the assumptions of Bishop and Davy (1985).

Vegetative reproduction varied greatly between rosettes. A rosette could produce daughter rosettes with or without producing stolons. Most rosettes which produced more than one daughter produced one axillary daughter with the rest on stolons. This maintains the parent's occupancy of space as well as contributes to the spread of the patch. Rarely, a rosette might produce 2 axillary daughters. With few exceptions, all rosettes initiated a visible inflorescence before daughter production.

Daughter and stolon production became visible shortly after rosettes had initiated inflorescences and continued throughout the summer. Peak stolon and daughter production occurred between January and February (Figure 2.1). Of all rosettes which initiated inflorescences, 76% produced one or more daughter rosettes and 46% produced one or more stolons. Of those rosettes which produced daughters, the average number of daughters per rosette was 1.6 with the maximum number for any one rosette being 4. A total of 846 daughters were produced by mapped rosettes. Both immigration and emigration of daughter rosettes occurred, resulting in a net immigration of 32 daughters, or 3.6% of the 878 mapped daughters within all quadrats. There was an average of 1.3 stolons per stolon-producing rosette with the average stolon length being 2.2 cm. The average distance of a daughter, including both stoloniferous and axillary, from its parent rosette was 1.1 cm. Of all daughters produced, 49% were axillary.

The overall mortality of *H. pilosella* within the quadrats was high. Of the 3343 rosettes and 878 daughters recorded, only 2540 (60%) survived to the following year. 41% of this mortality can be explained by the death of rosettes following reproduction and 6% by daughter reproduction leaving 53% unexplained. An overall decrease of 24% in the population occurred. However, this was almost entirely due to death in the treatment plots as control plots showed an increase of 3% for the 1994/95 year.

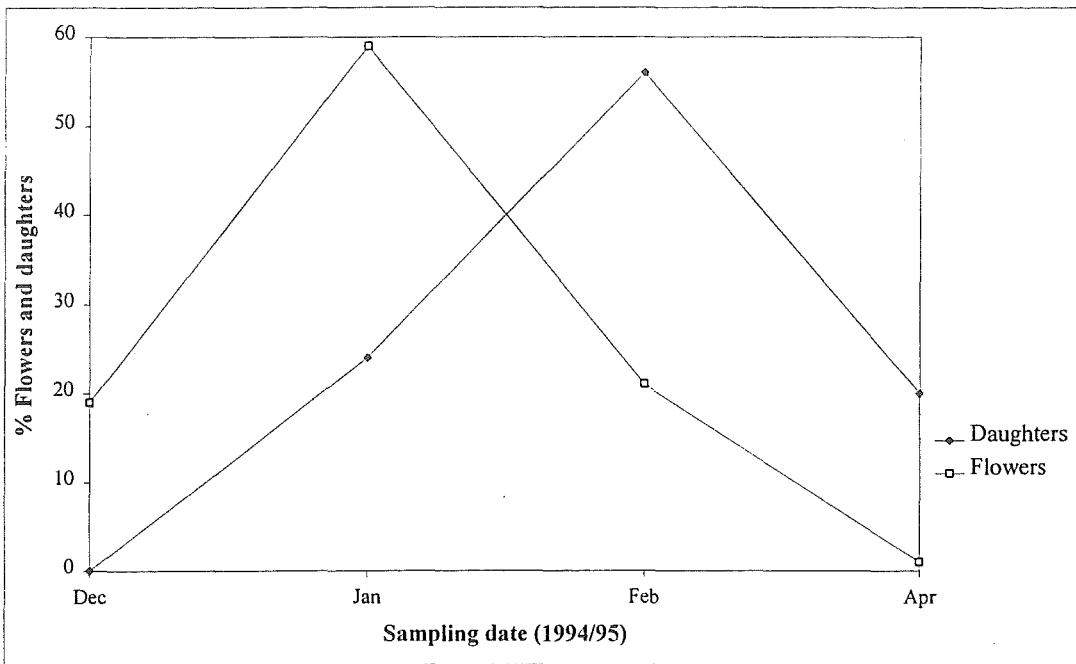


Figure 2.1 Timing of flowering and daughter production measured as the percentage of the totals during the 1994/95 growing season at Mt. John.

The average total vegetation cover per plot during February 1995 ranged from 28% to 100% with an overall average of 70%. Average *H. pilosella* cover ranged from 26% to 95% with an overall average of 49%. By February 1996 the overall average cover had increased to 65% *H. pilosella* and 86% total cover. The greatest change occurred within the fertilised and watered plots. Within these plots the *H. pilosella* rosettes increased in size considerably causing the plants to lose their flat rosette form. Rosettes became very crowded with their leaves tightly packed together vertically. In addition to the increase in rosette size, white clover (*Trifolium repens*) had either immigrated into the subplots, sprouted from a seed bank or increased in cover within these subplots rapidly increasing its cover over *H. pilosella* (Figure 2.2).

Results for the control and fungicide-only plots show that these populations changed little between 1994/95 and 1995/96. The total rosette population in the plots increased slightly from 441 rosettes in 1994 to 454 rosettes in 1995 and to 467 rosettes in 1996. This increase in density during the 1994/95 season is opposite to the decline within the other treatment plots. The change in cover in the control and fungicide-only plots was similar to that found in all plots combined; during 1995 the percent cover of *H. pilosella* was 37% with a total cover of 61% and in 1996 the cover increased to 55% *H. pilosella* cover and 73% total cover.

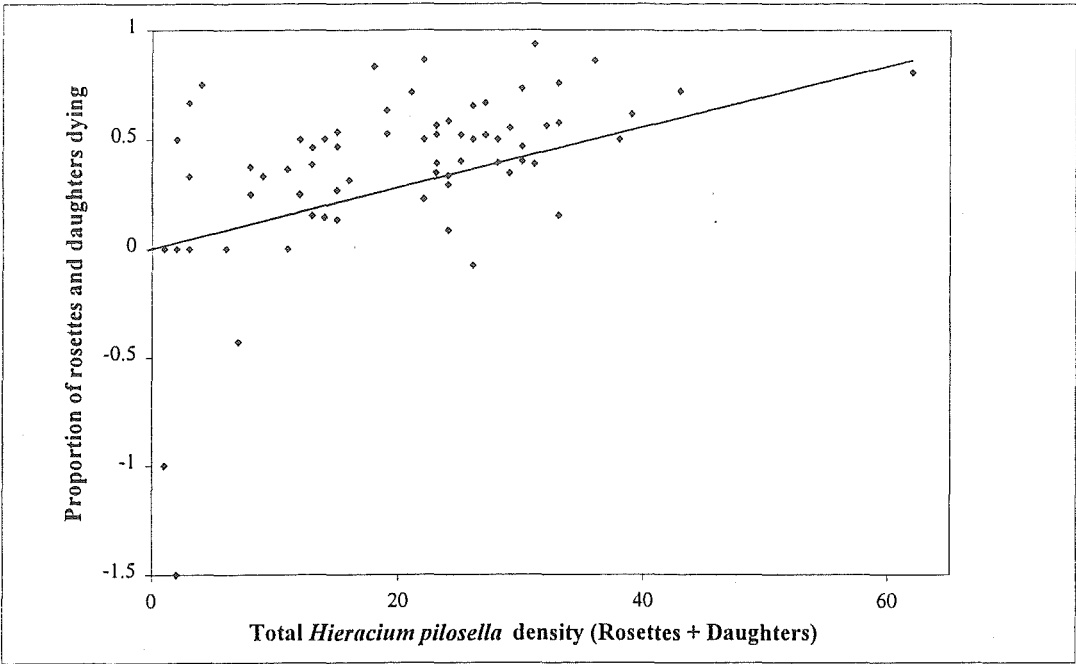


(a) Photo taken February 1995 before *Trifolium repens* was detected in the quadrat.

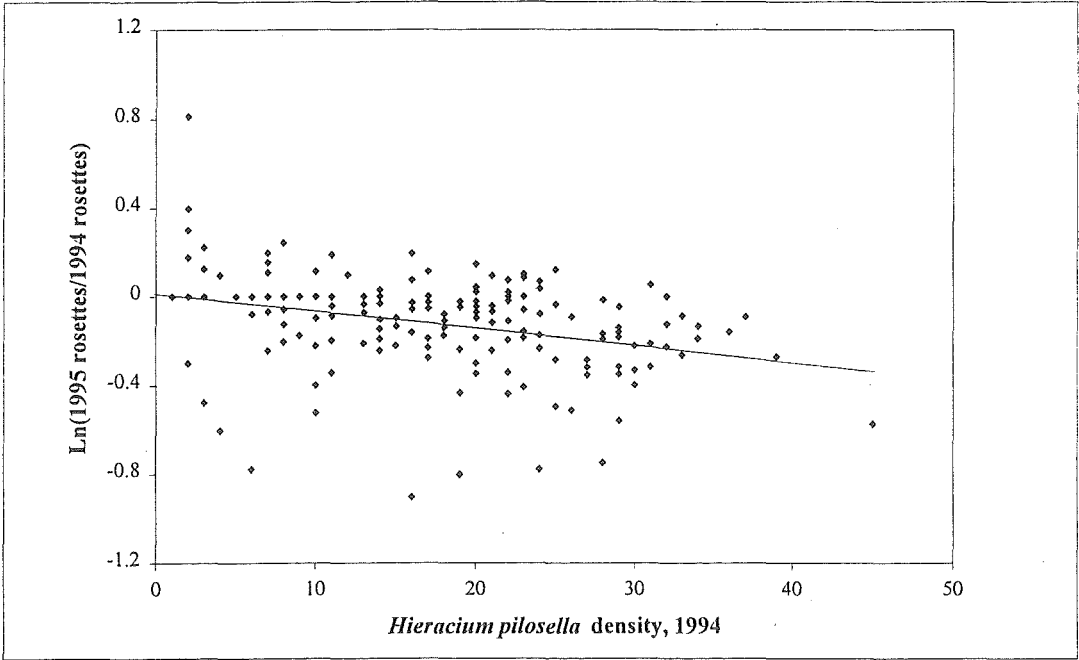


(b) Photo taken February 1996 when *Trifolium repens* was well established in quadrat.

Figure 2.2 The influx of *Trifolium repens* into quadrats over the period of this study. The photos are of the same quadrat one year apart (Plot G24, subplot 3/1, water + fertiliser).



(a) Regression for mortality vs. total density (n = 203). ANCOVA and regression equation shown in Table 2.2. Apparent negative mortality occurred due to the immigration of *Hieracium pilosella* daughter rosettes from surrounding areas.



(b) Regression for $\ln(1995 \text{ rosettes}/1994 \text{ rosettes})$ vs. initial rosette density (n = 199). ANCOVA and regression equation shown in Table 2.5

Figure 2.3 Effect of initial *Hieracium pilosella* density (December 1994) on mortality and population increase between December 1994 and December 1995.

2.3.2 Density-dependence in *Hieracium pilosella* population dynamics

H. pilosella density within the quadrats ranged from 1800 - 6633 rosettes/m² with an overall average of 3188 rosettes/m². Rosette density had little effect on most population parameters, but total mortality (based on original rosettes + daughter rosettes) was positively related to density (Figure 2.3a, Table 2.2). In addition, when non-reproductive mortality was analysed separately, it was significantly affected by density (Table 2.3).

Table 2.2 ANCOVA and regression equation for the proportion of *Hieracium pilosella* rosettes and daughters dying. *** *p* < 0.001

Source of Variation	df	Adj. MS	F
Rosette + daughter density	1	4.5039	32.58***
Plot	31	0.2046	1.48 ns
Error	170	0.1382	
$\left[\begin{array}{l} \text{Proportion of rosettes} \\ \text{and daughters dying} \end{array} \right] = 0.0139 \left[\begin{array}{l} \text{Parent + daughter} \\ \text{rosettes / 49 cm}^2 \end{array} \right] + 0.0031$			

Table 2.3 ANCOVA and regression equation for the proportion of non-reproductive *Hieracium pilosella* rosettes and daughters dying. *** *p* < 0.001

Source of Variation	df	Adj. MS	F
Rosette + daughter density	1	3.9390	16.85***
Plot	31	0.2962	1.27 ns
Error	179	0.2338	
$\left[\begin{array}{l} \text{Proportion of} \\ \text{non - reproductive} \\ \text{rosettes and daughters dying} \end{array} \right] = 0.012 \left[\begin{array}{l} \text{Parent + daughter} \\ \text{rosettes / 49 cm}^2 \end{array} \right] - 0.079$			

Apparent negative mortality occurred due to the immigration of *H. pilosella* daughter rosettes from surrounding areas. While no seedlings survived, the occurrence of seedlings within the plots decreased with rosette density (Table 2.4). Overall population change from October 1994 to October 1995 was also negatively related to initial rosette density (Figure 2.3b, Table 2.5). The proportion of rosettes initiating inflorescences was

not affected by initial rosette density ($n = 201$, $F = 0.91$, $p = 0.342$) but the proportion of daughters initiating inflorescences was: in the higher-density quadrats, there was a greater chance of a daughter rosette at least initiating an inflorescence (Figure 2.4, Table 2.6). Other variates which were not affected by initial rosette density included proportion of rosettes producing daughters (Figure 2.5), proportion of rosettes successfully flowering (Figure 2.6), overall number of daughters produced per rosette ($n = 201$, $F = 1.31$, $p = 0.26$), stolon number ($n = 201$, $F = 0.13$, $p = 0.72$), daughter distance ($n = 148$, $F = 2.23$, $p = 0.138$) and stolon length ($n = 199$, $F = 0.37$, $p = 0.541$).

Table 2.4 ANCOVA and regression equation for *Hieracium pilosella* seedlings per rosette with initial rosette density (1994) as the covariate. ** $p < 0.01$

Source of Variation	df	Adj. MS	F
Rosette density	1	0.0844	8.33**
Plot	31	0.0132	1.30 ns
Error	168	0.0101	
Seedlings = 0.064 - 0.0025(rosettes)			

Table 2.5 ANCOVA and regression equation for population change (log scale) of *Hieracium pilosella* with initial rosette density (1994) as the covariate. *** $p < 0.001$

Source of Variation	df	Adj. MS	F
Rosette density	1	4.3295	17.78***
Plot	31	0.3275	1.34 ns
Error	167	0.2436	
$\text{Ln} \frac{1995 \text{ rosettes}}{1994 \text{ rosettes}} = 0.0121 - 0.00775(\text{rosettes})$			

When density relationships were investigated in the control and fungicide plots only, rosette density remained a significant determinant of population mortality:

$$\left[\begin{array}{l} \text{Proportion of rosettes} \\ \text{and daughters dying} \end{array} \right] = 0.0043 + 0.0059 \left[\begin{array}{l} \text{Parent + daughter} \\ \text{rosettes / 49 cm}^2 \end{array} \right]$$

$n = 29$, $F = 7.58$, $p = 0.011$

However, the log ratio of population change ceased to be dependent on density ($n = 29$, $F = 0.79$, $p = 0.384$) as did the occurrence of seedlings ($n = 30$, $F = 1.45$, $p = 0.240$).

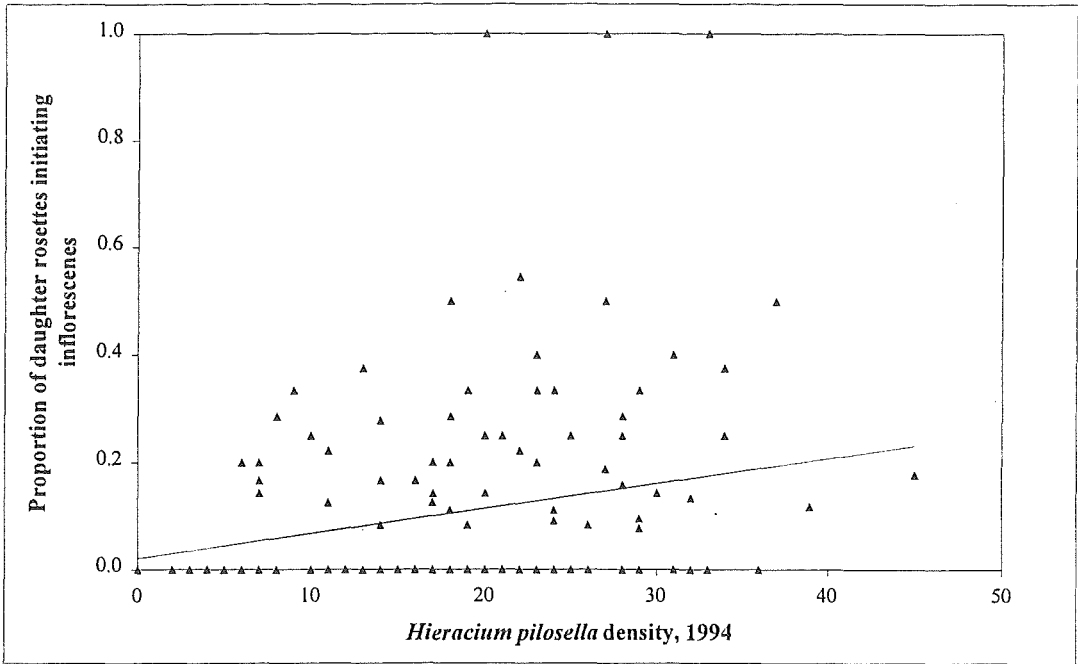


Figure 2.4 Regression for daughter inflorescence initiation vs. initial *Hieracium pilosella* density (per 49 cm²). ANCOVA and regression equation shown in Table 2.6.

Table 2.6 ANCOVA and regression equation for *Hieracium pilosella* daughter rosette inflorescence initiation with initial rosette density (1994) as the covariate.
** $p < 0.01$ and *** $p < 0.001$

Source of Variation	df	Adj. MS	F
Rosette density	1	0.1999	8.20**
Plot	31	0.0567	2.33***
Error	120	0.0244	
<div> <div> <div>Proportion of daughters</div> <div>initiating inflorescences</div> </div> <div>= 0.021 + 0.0047[Rosettes]</div> </div>			



Figure 2.5 Proportion of *Hieracium pilosella* rosettes producing daughters (triangles). Filled squares are means based on the grouping of initial rosette density (0 - 5, 6 - 10, 11 - 15, ... , 36 - 45). Vertical bars show \pm 95% confidence intervals for the means and n = number of rosettes within each density group. Density had no significant effect.

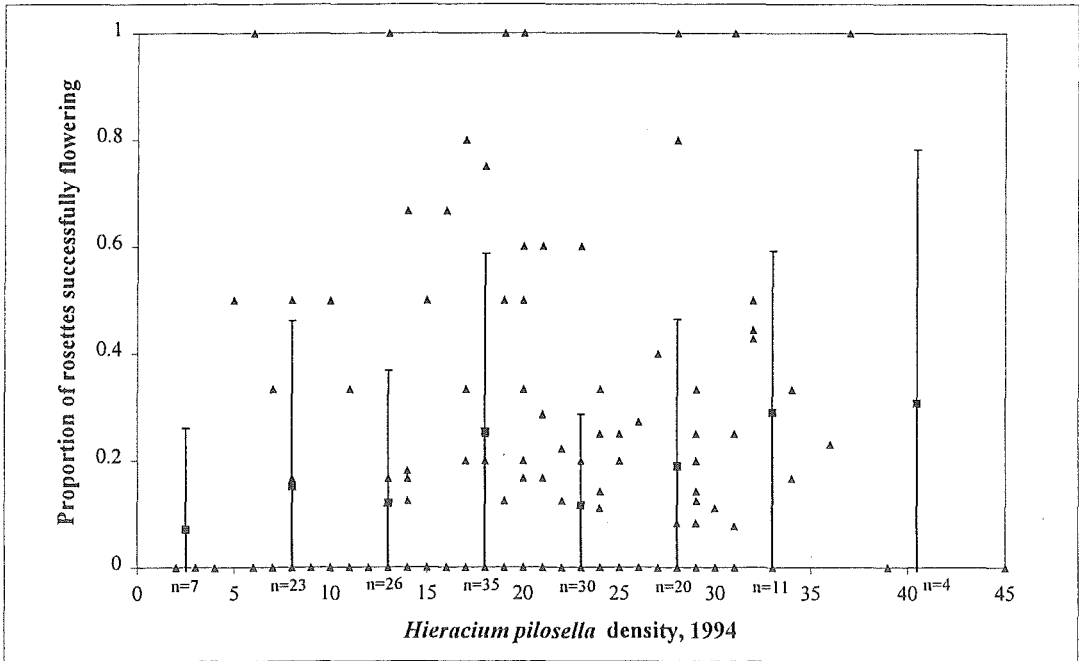


Figure 2.6 Proportion of *Hieracium pilosella* rosettes successfully flowering (triangles). Filled squares are means based on the grouping of initial rosette density (0 - 5, 6 - 10, 11 - 15, ... , 36 - 45). Vertical bars show \pm 95% confidence intervals for the means and n = number of rosettes within each density group. Density had no significant effect.

Table 2.7 ANCOVA and regression equations for the effect of % *Hieracium pilosella* cover on various demographic parameters. ** $p < 0.01$ and *** $p < 0.001$

(a) Proportion of rosettes and daughters which died over the 1994/95 season.

Mortality			
Source of Variation	df	Adj. MS	F
% <i>H. pilosella</i> cover	1	1.6462	10.61***
Plot	31	0.2341	0.053ns
Error	169	0.1551	
$\left[\begin{array}{l} \text{Proportion of rosettes} \\ \text{and daughters dying} \end{array} \right] = -7.025 + 0.143 \left[\begin{array}{l} \% \text{ } H. \text{ pilosella} \\ \text{cover} \end{array} \right]$			

(b) Average stolon length within plots.

Stolon Length			
Source of Variation	df	Adj. MS	F
% <i>H. pilosella</i> cover	1	10171.7	73.79***
Plot	31	208.2	1.51ns
Error	178	137.8	
$\left[\begin{array}{l} \text{Average stolon} \\ \text{length} \end{array} \right] = -0.221 + 0.231 \left[\begin{array}{l} \% \text{ } H. \text{ pilosella} \\ \text{cover} \end{array} \right]$			

(c) Proportion of rosettes which produced stolons within plots.

Stolons Produced			
Source of Variation	df	Adj. MS	F
% <i>H. pilosella</i> cover	1	0.3618	29.00***
Plot	31	0.0150	1.20ns
Error	167	0.0125	
$\left[\begin{array}{l} \text{Proportion of rosettes} \\ \text{producing stolons} \end{array} \right] = 0.0127 + 0.0015 \left[\begin{array}{l} \% \text{ } H. \text{ pilosella} \\ \text{cover} \end{array} \right]$			

Table 2.7 continued

(d) Proportion of rosettes which produced daughters within plots.

Daughters Produced			
Source of Variation	df	Adj. MS	F
% <i>H. pilosella</i> cover	1	0.3590	17.23***
Plot	31	0.0271	1.30ns
Error	167	0.0208	
$\left[\begin{array}{l} \text{Proportion of rosettes} \\ \text{producing daughters} \end{array} \right] = 0.0787 + 0.0015 \left[\begin{array}{l} \% \text{ } H. \text{ pilosella} \\ \text{cover} \end{array} \right]$			

(e) Proportion of rosettes which initiated inflorescences within plots.

Inflorescence Initiation			
Source of Variation	df	Adj. MS	F
% <i>H. pilosella</i> cover	1	0.61071	23.78***
Plot	31	0.02890	1.13ns
Error	167	0.02568	
$\left[\begin{array}{l} \text{Proportion of rosettes} \\ \text{initiating inflorescences} \end{array} \right] = 0.194 + 0.0019 \left[\begin{array}{l} \% \text{ } H. \text{ pilosella} \\ \text{cover} \end{array} \right]$			

(f) Number of seedlings per rosette initiated during the 1994/95 season.

Seedlings			
Source of Variation	df	Adj. MS	F
% <i>H. pilosella</i> cover	1	0.0897	8.84**
Plot	31	0.0135	1.33ns
Error	167	0.0102	
$\left[\begin{array}{l} \text{Seedlings per} \\ \text{rosette} \end{array} \right] = 0.0202 - 0.0074 \left[\begin{array}{l} \% \text{ } H. \text{ pilosella} \\ \text{cover} \end{array} \right]$			

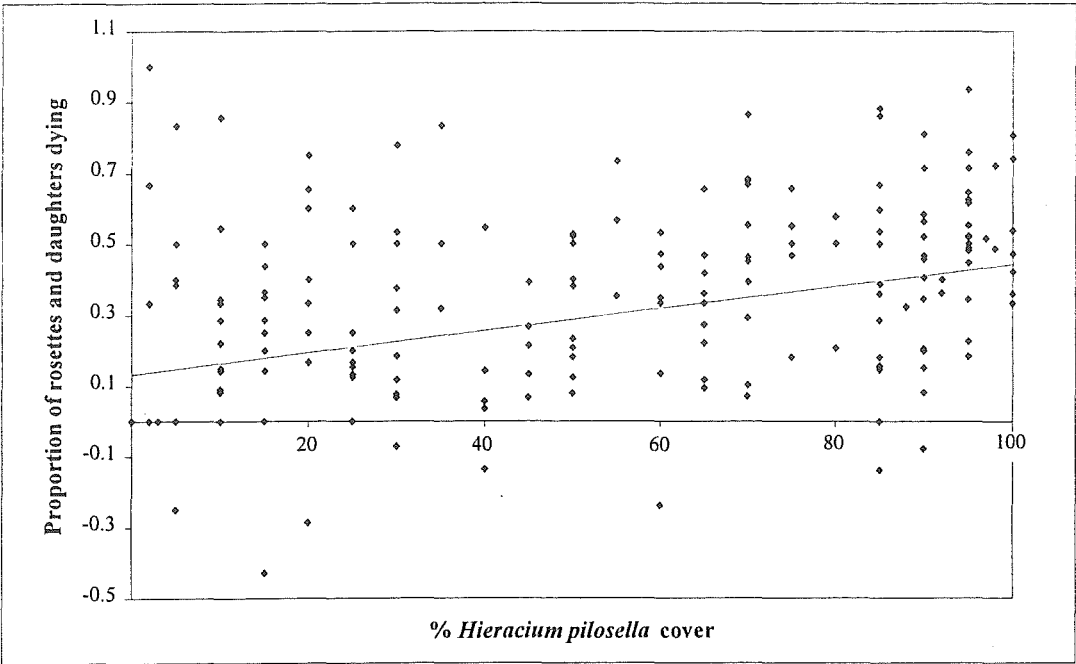


Figure 2.7 The effect of *Hieracium pilosella* cover on population mortality. Regression of mortality against % *H. pilosella* cover (per 49 cm²). ANCOVA and regression equation shown in Table 2.7a.

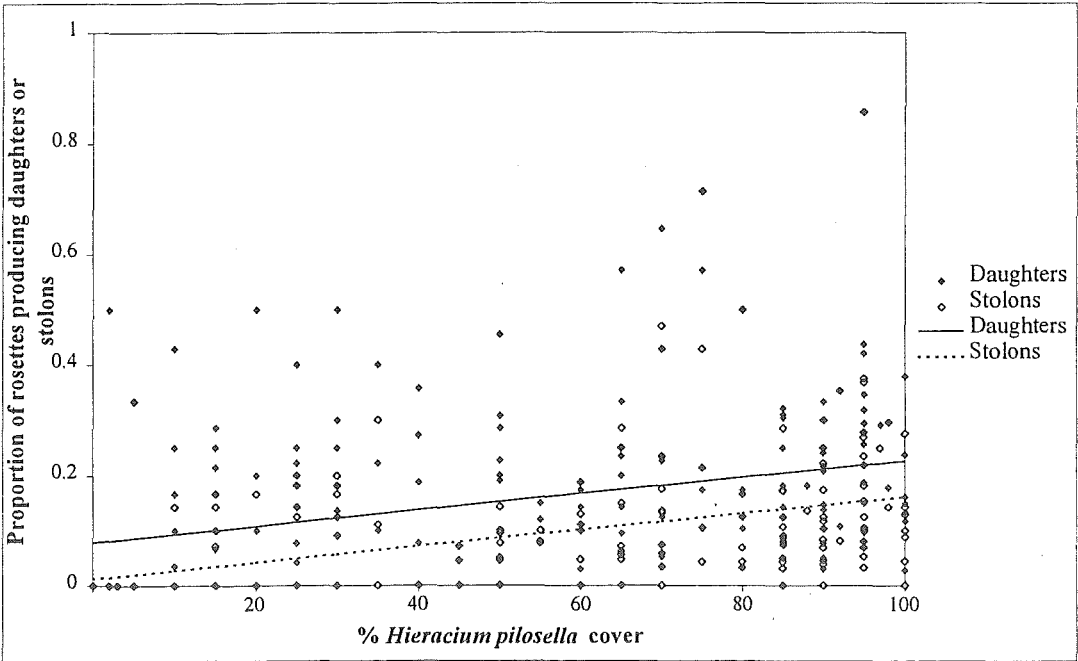


Figure 2.8 The effect of *Hieracium pilosella* cover on daughter and stolon production. Regressions of stolon or daughter production against % *H. pilosella* cover (per 49 cm²). ANCOVAs and regression equations shown in Table 2.7c and d.

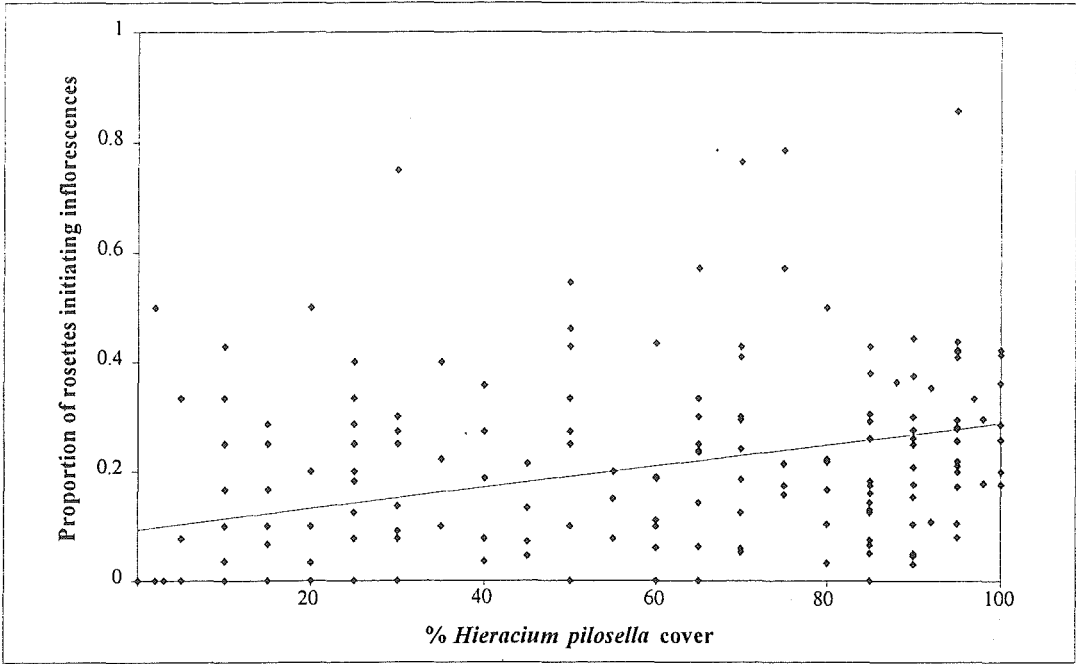


Figure 2.9 The effect of *Hieracium pilosella* cover on rosette inflorescence initiation. Regression of inflorescence initiation for rosettes against % *H. pilosella* cover (per 49 cm²). ANCOVA and regression equation shown in Table 2.7e.

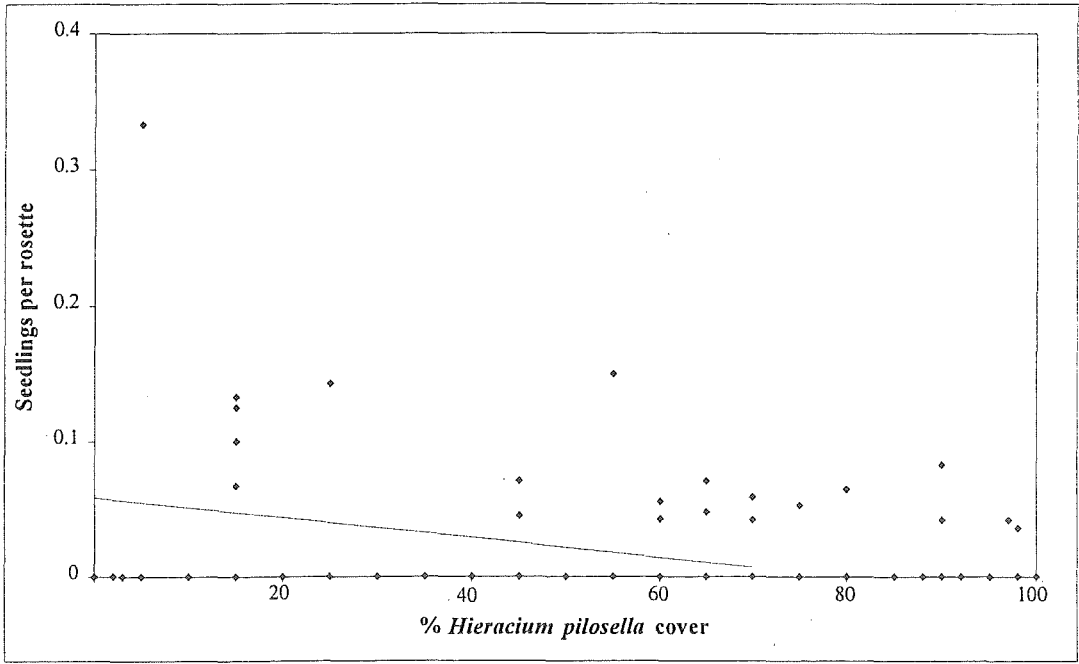


Figure 2.10 The effect of *Hieracium pilosella* cover on seedling establishment. Regression of seedlings per rosette against % *H. pilosella* cover (per 49 cm²). ANCOVA and regression equation shown in Table 2.7f.

2.3.3 Relationships between *Hieracium pilosella* population parameters and cover

To investigate density-dependence further, ANCOVAs were run with percent cover of *H. pilosella* as the predictor. Mortality, average stolon length, percent of rosettes producing stolons or daughters, proportion of rosettes initiating inflorescences, and seedlings per rosette were significantly related to percent cover (Table 2.7a - f). Mortality of rosettes and daughters increased with increasing *H. pilosella* cover (Figure 2.7) as did average stolon length, proportion of rosettes producing daughters or stolons (Figure 2.8) and proportion of rosettes initiating inflorescences (Figure 2.9). The number of seedlings per rosette decreased as cover increased (Figure 2.10). There were no relationships between *H. pilosella* cover and the success of flowering for either daughters or rosettes ($n = 156$, $F = 0.62$, $p = 0.431$; $n = 60$, $F = 0.29$, $p = 0.596$ respectively), mean number of daughters or stolons per reproductive rosette ($n = 149$, $F = 0.05$, $p = 0.832$; $n = 114$, $F = 3.24$, $p = 0.075$ respectively), or distance from parent to daughter ($n = 148$, $F = 3.83$, $p = 0.053$).

Table 2.8 *Hieracium pilosella* demographic parameters which were found to have no association with % cover of other species.

Parameter	n	F	p
Mortality	202	1.83	0.178
Seedlings	200	1.48	0.225
% Stolon producing rosettes	200	2.71	0.102
Rosette inflorescence initiation	200	2.84	0.094
Daughter inflorescence initiation	60	0.53	0.473
Daughter production	200	2.97	0.086
Flowering success in rosettes	200	0.01	0.938
Flowering success in daughters	153	0.33	0.568
Daughters per rosette	149	1.35	0.248
Stolons per rosette	114	1.27	0.263
Mean daughter distance	148	0.24	0.624

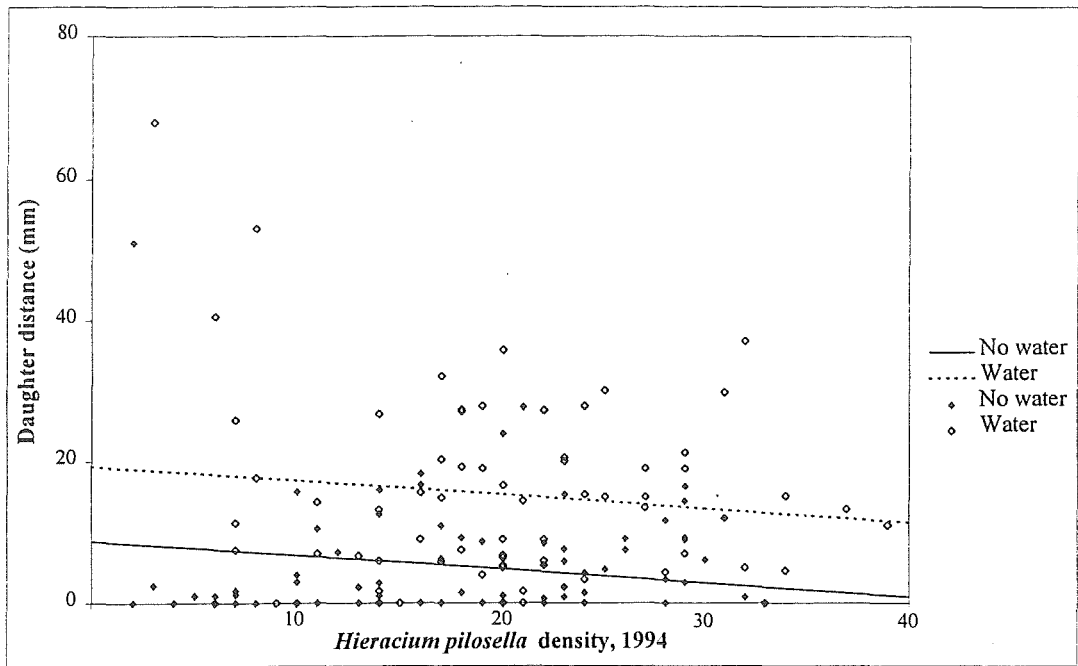
The cover of other species within the quadrats at the start of the 1994 growing season was low, ranging from 1% - 48% with an overall average of 22%. The bulk of this cover consisted of *Festuca novae-zelandiae*, *Erythranthe pumila* and *Trifolium repens*. To investigate the possibility of competition between *H. pilosella* and other species, ANCOVAs were run using percent cover of other species as the covariate. Of all the demographic parameters tested, none were found to have any significant relationship with cover (Table 2.8).

2.3.4 Treatment effects on *Hieracium pilosella* population dynamics

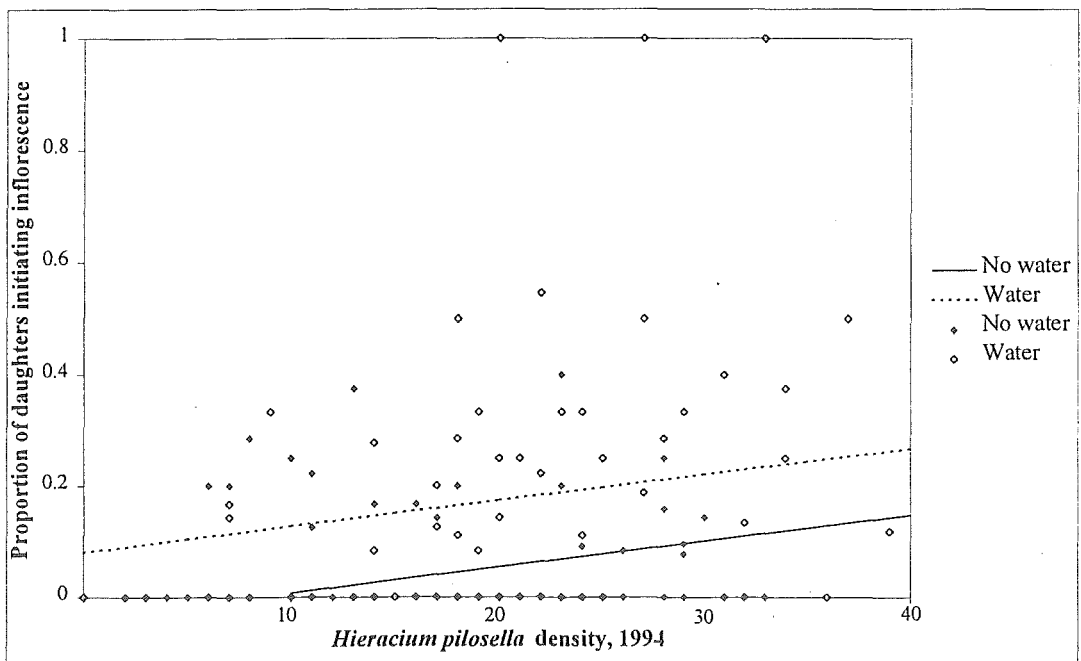
Water and fertiliser had the greatest effect on the population dynamics of *H. pilosella* (Table 2.9). There was a negative relationship between the proportion of aborted inflorescences in rosettes and the water treatment, with greater abortion occurring in the un-watered plots. There was a three-fold increase in daughter distance and daughter inflorescence initiation when water was added to the plots (Figure 2.11a, b) and the proportion of daughters which were stoloniferous doubled. There were also significantly more emigrating daughters in the watered plots, as would be expected from the longer stolon lengths.

Adding fertiliser increased the average stolon length and the proportion of rosettes which produced stolons. Stolon length increased from an average of 8.4 mm to 14.5 mm while stolon production increased from 6.5% to 13.5% of rosettes. In addition, the proportion of rosettes initiating inflorescences increased significantly in the fertiliser plots (Figure 2.12) as did the proportion of rosettes producing daughters and/or stolons. Finally, the mean number of daughters produced by reproductive rosettes increased from 1.46 to 1.73.

As would be expected, the cutting treatment decreased the proportion of rosettes successfully flowering, however, there was no statistically significant effect on flowering success in daughters (Table 2.9). Cutting increased the proportion of rosettes producing stolons from 8% to 12%.



(a) Regressions for daughter distance on density. $n = 30$, $dd = -0.1973 r + 10.55 w + 8.75$ where r = initial rosette density, $w = 0$ for no water, 1 for water and dd = average daughter distance from parent rosette.



(b) Regressions for daughter inflorescence initiation on density. $n = 30$, $dr = 0.00467 r + 0.12 w - 0.0392$ where r = initial rosette density, $w = 0$ for no water or 1 for water and dr = proportion of daughters which initiated an inflorescence.

Figure 2.11 The effect of the water treatment on daughter distance and daughter inflorescence initiation. Rosette density is number of rosettes per 49 cm².

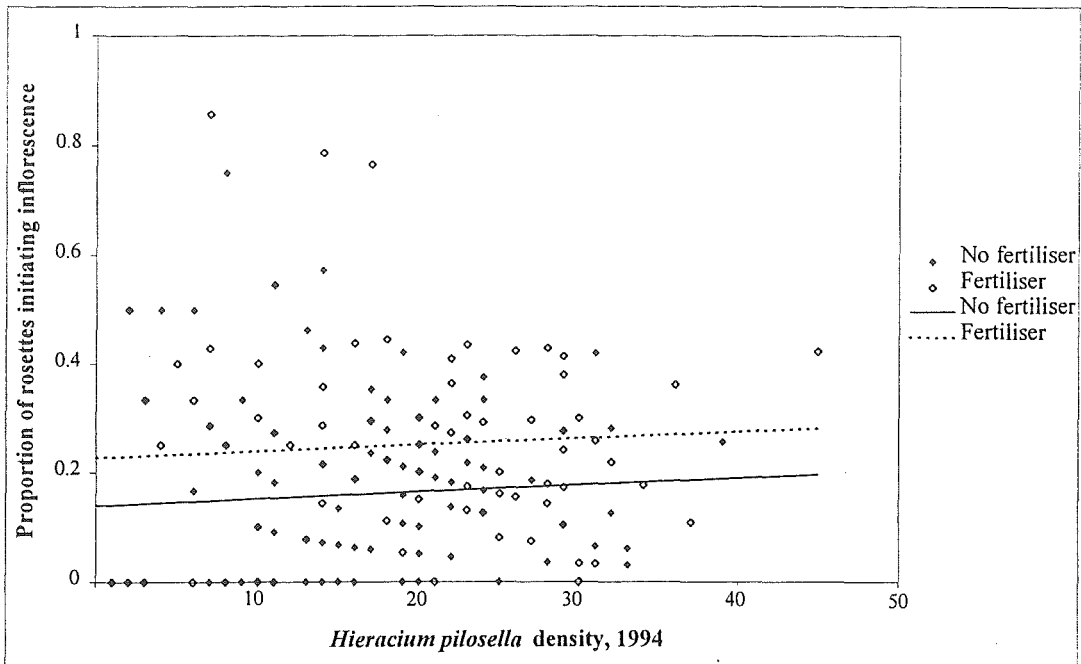


Figure 2.12 Regressions for inflorescence initiation in rosettes on density for fertilised and unfertilised plots. $n = 30$, $iir = 0.00128 r + 0.087 f + 0.1387$ where iir = proportion of rosettes which initiate inflorescences, r = initial rosette density, and $f = 0$ for no fertiliser or 1 for fertiliser. Rosette density is number of rosettes per 49 cm^2 .

The fungicide/insecticide treatment had no significant effects on any of the population parameters. The addition of the fungicide/insecticide treatment was helpful to verify that these chemicals would have no effect *per se* with regard to their potential use in determining the effectiveness of any future biological control agents. So, in terms of the present trial, the fungicide/insecticide treatment was hereafter included with the control plots as additional replicates.

The water \times fertiliser interaction had a slightly significant effect on the mortality rate ($p = 0.042$). The rate of mortality increased in the +water/-fertiliser and -water/+fertiliser treatments but no additional increase occurred in the +water/+fertiliser compared to either treatment alone (Table 2.10a). The number of stolons per rosette was also affected by the water \times fertiliser interaction ($p = 0.034$); while there was an increase in stolons per rosette with both water alone and fertiliser alone, the increase was greater when both were added (Table 2.10b).

Table 2.9 Treatment means (adjusted for covariate) and *p*-values for the effect of four environmental treatments on various demographic parameters in *Hieracium pilosella* at Mt. John, 1994/95. - = without treatment, + = with treatment, R = Number of rosettes for given year. Covariate is initial rosette density unless indicated by "*" in which case Covariate = initial rosette + daughter density.

Variate	- Water	+ Water	<i>p</i>	- Fert.	+ Fert.	<i>p</i>	- Cut	+ Cut	<i>p</i>	- Fung.	+ Fung.	<i>p</i>
Dtr. Distance	5.09	15.64	<0.001	8.42	12.31	0.064	10.39	10.35	0.983	9.58	11.16	0.428
Avg. stolon length	7.04	15.83	<0.001	8.39	14.48	0.008	11.31	11.56	0.904	11.48	11.39	0.966
Proportion of rosettes initiating inflorescence	0.181	0.226	0.099	0.160	0.247	0.005	0.184	0.223	0.154	0.218	0.189	0.269
Flowering success in rosettes	0.195	.0192	0.962	0.247	0.140	0.095	0.281	0.106	0.011	0.193	0.194	0.984
Aborted rosettes	0.566	0.365	0.002	0.434	0.497	0.254	0.453	0.478	0.649	0.499	0.431	0.219
Proportion of daughters initiating inflorescence	0.046	0.166	<0.001	0.079	0.133	0.068	0.106	0.106	0.993	0.079	0.133	0.068
Flowering success in daughters	0.054	0.073	0.795	0.043	0.084	0.568	0.072	0.055	0.809	0.046	0.081	0.631
Aborted daughters	0.492	0.428	0.595	0.445	0.474	0.806	0.588	0.331	0.052	0.481	0.438	0.717
Proportion of rosettes producing daughters	0.152	0.175	0.304	0.121	0.206	0.002	0.143	0.183	0.090	0.176	0.151	0.268
Mean no. of daughters	1.602	1.593	0.923	1.460	1.734	0.008	1.611	1.583	0.761	1.672	1.522	0.115
Mean no. stolons	1.218	1.317	0.216	1.229	1.306	0.327	1.213	1.322	0.172	1.305	1.230	0.340
Stoloniferous daughters	0.310	0.616	<0.001	0.432	0.494	0.199	0.442	0.484	0.375	0.451	0.475	0.618
Proportion of rosettes producing stolons	0.0615	0.139	<0.001	0.065	0.135	<0.001	0.081	0.120	0.022	0.117	0.084	0.051
Mortality *	0.245	0.342	0.124	0.234	0.354	0.063	0.254	0.333	0.201	0.308	0.279	0.626
Proportion of daughters emigrating *	0.052	0.171	0.004	0.078	0.145	0.070	0.112	0.111	0.977	0.124	0.099	0.487
R95/R94	0.910	0.779	0.104	0.899	0.790	0.171	0.898	0.791	0.177	0.825	0.864	0.617

Table 2.10 Two-way interaction between fertiliser and water ($p < 0.05$ in all cases). Only mean values are presented because standard errors of these treatments are affected by other treatments (i.e. cutting) because of the factorial design.

(a) Mortality of rosettes and daughter rosettes.

Treatment	- Water	+ Water
- Fertiliser	0.119	0.349
+ Fertiliser	0.371	0.336

(b) Average number of stolons per rosette.

Treatment	- Water	+ Water
- Fertiliser	0.0393	0.1238
+ Fertiliser	0.1071	0.2790

The fertiliser \times cutting interaction effect on stolon production was barely significant ($p = 0.049$) with the proportion of rosettes producing stolons increasing from 0.06 in the unfertilised, uncut plots to 0.10 in the fertilised \times cut interaction plots (Table 2.11a). The addition of either fertiliser or cutting generally increased stolon production although the greatest increase occurred when both were applied together. The two-way interaction of fertiliser and cutting also had an effect on the number of stolons per rosette ($p = 0.013$) and the proportion of daughter rosettes which initiated inflorescences ($p = 0.020$). Both fertiliser and cutting increase the number of stolons per rosette with the greatest increase occurring when both treatments were applied (Table 2.11b). In the absence of the other, both fertiliser and cutting decreased the proportion of daughter rosettes initiating inflorescences but when both cutting and fertiliser were applied, the proportion increased (Table 2.11c).

There were few significant effects from the three-way interaction of water, fertiliser and cutting. Cutting increased seedlings per rosette in the absence of water and fertiliser but when cutting was applied in addition to water and/or fertiliser this increase was much less (Table 2.12).

Table 2.11 Two-way interaction of fertiliser and cutting ($p < 0.05$ in all cases). Only mean values are presented because standard errors of these treatments are affected by other treatments (i.e. water) because of the factorial design.

(a) Proportion of rosettes producing stolons.

Treatment	- Fertiliser	+ Fertiliser
- Cutting	0.0622	0.0685
+ Cutting	0.0685	0.0994

(b) Average number of stolons per rosette.

Treatment	- Fertiliser	+ Fertiliser
- Cutting	0.0760	0.1342
+ Cutting	0.0872	0.2518

(c) Proportion of daughter rosettes which initiated inflorescences.

Treatment	- Fertiliser	+ Fertiliser
- Cutting	0.115	0.097
+ Cutting	0.043	0.168

Table 2.12 Number of seedlings per rosette of *Hieracium pilosella* as affected by the three-way interaction between water, fertiliser and cutting ($p = 0.050$).

Treatments	- Water		+ Water	
	- Fertiliser	+ Fertiliser	- Fertiliser	+ Fertiliser
- Cutting	0.0001	0.0093	0.0649	0.0258
+ Cutting	0.0685	0.0036	0.0195	0.0308

2.3.5 Treatment effects on plant cover

Comparisons between treated and untreated plots showed that the average cover of *H. pilosella* was significantly increased by fertiliser while the average cover of clover was increased most by water (Table 2.13).

Table 2.13 Treatment means and *p* values for the average cover (%) of *Hieracium pilosella* and *Trifolium repens* under the main treatment effects. Cover was estimated from photographs taken in February 1996, 1 ½ years after initial treatment application.

Variate	-Water	+Water	<i>p</i>	-Fert.	+Fert.	<i>p</i>	-Cut	+Cut	<i>p</i>
<i>Hieracium pilosella</i> % cover	68.13	65.16	0.372	53.99	79.30	<0.001	65.83	67.45	0.623
<i>Trifolium repens</i> % cover	0.78	12.12	<0.001	4.70	8.21	0.109	5.80	7.11	0.535

Both *H. pilosella* cover ($p = 0.013$) and *Trifolium repens* cover ($p < 0.001$) were affected by the two-way interaction of fertiliser and cutting (Table 2.14). The cover of *H. pilosella* increased slightly when the cutting treatment was applied in the absence of fertiliser but decreased with cutting applied in the presence of fertiliser. In contrast, the cover of *T. repens* decreased in the absence of fertiliser yet increased in the presence of fertiliser when cutting was applied. Fertiliser increased the cover of *H. pilosella* regardless of the cutting treatment whereas it only increased the cover of *T. repens* when applied in tandem with cutting (Table 2.14).

Table 2.14 Treatment means for the two-way interaction of fertiliser and cutting on the cover of *Hieracium pilosella* ($p < 0.05$) and *Trifolium repens* ($p < 0.001$) 1 ½ years after the initial application of treatments. Cover was estimated from photographs taken in February 1996.

Treatment	<i>Hieracium pilosella</i>		<i>Trifolium repens</i>	
	- Fertiliser	+ Fertiliser	- Fertiliser	+ Fertiliser
- Cutting	48.67	83.00	9.22	2.38
+ Cutting	59.31	75.60	0.18	14.04

The three-way interaction of water, fertiliser, and cutting significantly affected the cover of *H. pilosella* ($p = 0.004$) and *T. repens* ($p < 0.001$). The cutting treatment slightly increased the cover of *H. pilosella* in the absence of water. When water was added, cutting increased the cover in the absence of fertiliser but decreased it in the presence of fertiliser (Table 2.15a). As with *H. pilosella*, cutting had little effect on the cover of *T. repens* in the absence of water. But when water was applied the results are opposite to that seen in *H. pilosella*. Cutting caused a decrease in the cover of *T. repens* in the absence of fertiliser and an increase in the presence of fertiliser (Table 2.15b).

Table 2.15 Treatment means for the three-way interaction between water, fertiliser and cutting on the cover of *Hieracium pilosella* ($p < 0.01$) and *Trifolium repens* ($p < 0.001$) 1 ½ years after initial treatment application. Cover was estimated from photographs taken in February 1996.

(a) *Hieracium pilosella*

Treatments	- Water		+ Water	
	- Fertiliser	+ Fertiliser	- Fertiliser	+ Fertiliser
- Cutting	56.35	76.58	40.98	89.43
+ Cutting	57.97	81.62	60.66	69.57

(b) *Trifolium repens*

Treatments	- Water		+ Water	
	- Fertiliser	+ Fertiliser	- Fertiliser	+ Fertiliser
- Cutting	0.00	0.00	18.44	4.75
+ Cutting	0.00	3.13	0.36	24.95

The above results suggested that there might have been a negative correlation between the percent cover of *H. pilosella* and *T. repens*. When *T. repens* was regressed against *H. pilosella* cover across all plots, there was a significant negative relationship (Table 2.16).

Table 2.16 ANCOVA and regression equation for the relationship between *Hieracium pilosella* and *Trifolium repens* cover (%). *** $p < 0.001$

Source of Variation	<i>Trifolium repens</i> cover		
	df	Adj. MS	F
<i>H. pilosella</i> cover	1	6736.2	29.19***
Plot	31	17185.9	2.40***
Error	181	41770.3	
$[\% \text{ } T. \text{ repens cover}] = 18.62 - 0.20[\% \text{ } H. \text{ pilosella cover}]$			

2.3.6 Miscellaneous observations

While measurements were not made, the following were observed over the course of this study. There were areas within the study site which had been recently disturbed by rabbit diggings, soil cores and filled in holes. *H. pilosella* rosettes in these disturbed areas were generally larger in size than rosettes in non-disturbed areas. In addition, rosettes within the fertiliser and water + fertiliser treatment plots grew larger and developed into dense, tightly packed mats. Prior to the addition of water or fertiliser, bare ground was visible between individual rosettes but within 3 to 4 months these areas of bare ground began to disappear and by the start of the second growing season bare ground was almost non-existent (Figure 2.13).

During the second year of the study, the fertiliser and water treatments were continued even though the plots were not being used for demographic data collection. During December and January of this period there was a visual difference in the abundance of *H. pilosella* inflorescences. Those plots which had received the fertiliser or water + fertiliser treatments had noticeably more flowering plants than the plots which did not receive these treatments. This is consistent with the continuation of the flower-promoting effects of water and fertiliser seen in the first year (Table 2.9).



(a) February 1995



(b) February 1996

Figure 2.13 The effect of water and fertiliser on *Hieracium pilosella* growth. Photos are typical representations of the disappearance of bare ground after one year's growth in plots which received fertiliser alone or both water and fertiliser together. Plot G26, quadrat 29/2, fertiliser treatment.

2.4 Discussion

2.4.1 General population features

Makepeace (1985a) suggested that mortality in *Hieracium pilosella* was almost exclusively restricted to reproductive rosettes. If reproduction were density-dependent, with less reproduction occurring at higher densities as he suggested, one would expect to find a corresponding increase in the proportion of reproductive rosettes and hence mortality due to reproduction with decreased density. This was not the case in this study. Fifty-three percent of the mortality found within the quadrats could not be attributed to rosette or daughter reproduction. Even considering only the unamended plots, mortality was not restricted to reproduction. In some of the un-watered plots, rosette death could be attributed to drought stress caused by hot north-westerly winds while for other plots the causes of rosette death could not be determined.

Other studies (Makepeace 1985a; Bishop & Davy 1994; McIntosh, Loeseke & Bechler 1995; Espie & Boswell unpublished manuscript) describe patches of *H. pilosella* surrounded by a bare halo area and in older patches a dead or sparse central region. There are few distinguishable patches at the Mt. John site, probably as a result of the long history of *H. pilosella* in the area. Any original patches may have grown together, become intermingled and senesced to produce the patterns which exist today (i.e. Mt. John is all sparse central regions). Several observers have shown that soils under *H. pilosella* patches are more acidic (Makepeace 1985a; McIntosh *et al.* 1995; Espie & Boswell unpublished manuscript). McIntosh *et al.* (1995) found that the halo of smaller patches is lower in nutrients than patch centres and suggests that as patches expand, the advantage of nutrient uptake from the halo zone is likely to become limited to patch margins since the centre becomes progressively further from this region. If this is true and the *H. pilosella* population at Mt. John has expanded such that all recognisable patches have disappeared then it may be that *H. pilosella* has uniformly depleted soil resources so that no rosettes are gaining benefits from being on a new patch edge.

2.4.2 Density

The *H. pilosella* population at the Mt. John trial site seems to have reached an equilibrium with little variation in population densities or cover. The density of the population has probably been in equilibrium for 2 or more decades since *H. pilosella*

cover has changed little since the 1960s (D. Scott, *pers. comm.*). This provided an excellent opportunity to study the dynamics within a mature population.

The density within the unamended plots changed little over the two years of this study hence the overall population decline encountered within the treatment plots can be attributed to the treatments themselves. This pattern of little density change in untreated plots but a decline in density with the addition of fertilisers and/or grazing was also found by Davy and Bishop in Breckland (1984). They attributed the rapid decline of *H. pilosella* populations in their treated plots to increased growth of competitor species with the addition of nutrients. The negative relationship between *H. pilosella* and *Trifolium repens* in this study suggests that competition may in part be responsible for the decline of *H. pilosella*, however, this hypothesis could not be verified (Chapter 5).

Density-dependent reproduction has been suggested as a general strategy for population regulation (Harper 1977) and has been detected in some plant populations (e.g. Putwain, Machin & Harper 1968; Thomas & Dale 1974; Barkham 1980; Thompson & Beattie 1981). Makepeace (1985a) attributed the increase in *H. pilosella* reproduction on patch edges to the lower rosette density of edges as compared to the centre of patches. In studies in Breckland (Bishop *et al.* 1978; Bishop & Davy 1984 & 1985), the probability of flowering and the probability of producing a daughter rosette decreased with increasing density, as did stolon production. The same studies found that inflorescence abortion was higher when density increased. None of these density-dependent reproductive relationships were found in the Mt. John population. One possible explanation may lie in the general condition of the population at this site. In comparison to the reproductive activity at Makepeace's sites (excluding Sawdon) inflorescence initiation at Mt. John was low, hence there was little opportunity for a density-dependent response via flowering. *H. pilosella* has been present at high levels over a long period of time and may have reached carrying capacity. With the exception of plants re-colonising disturbed areas such as rabbit diggings, the rosettes are generally small (*pers. obs.*), whereas rosettes in areas which have not had such a long *H. pilosella* history often have a more lush appearance. The environment at Mt. John may have become so unfavourable in some way (e.g. nutrient depletion, drought, allelopathy) that the plants are limited by

environmental conditions rather than intraspecific competition. This hypothesis was tested in a glasshouse experiment and is described in Chapter 4.

A second explanation for the lack of density-dependent reproduction at the Mt. John trial site may lie in the quadrat size of the study. While rosette density between quadrats varied greatly, this variation was based on small areas (49 cm²). On a larger scale densities were less variable. If quadrat size were too small, one would not expect to detect any differences based on population density if plants were affected by average density on the scale of our plots (1.2 × 1.2 m). However, because of their sedentary nature, plants can be greatly affected by their immediate surroundings by way of local environmental conditions and biotic interactions with nearest neighbours (Harper 1977). There have been several studies on plant species which have shown that spatially local interactions have an effect on the dynamics and structure of a community (e.g. Turkington & Harper 1979; Weiner & Conte 1981; Pacala & Silander 1990; Cain *et al.* 1995). On a small scale, density can be an indirect measure of neighbour distance and hence small quadrat size may not be responsible for the lack of reproductive density-dependence.

Density-dependent mortality is the only form of regulation which was found to occur at the Mt. John trial site regardless of treatment effects. Mortality and reproduction in *H. pilosella* are closely linked and yet less than half of the total mortality in the plots could be explained by reproduction suggesting that non-reproductive mortality is density-dependent. Harper (1977) suggests that plants can respond to density by phenotypic plasticity or mortality or both. In the case of mortality, if a plant population continues to reproduce at the same rate under high densities there most certainly would be a point where establishment space became sparse resulting in the death of offspring. In addition, higher densities may lead to more rosettes competing for limited resources.

In general, the occurrence of seedlings at Mt. John is rare (D. Scott, *pers. comm.*). Seedling germination was a rare event during the period of this trial and the establishment of seedlings was non-existent. This is in contrast to the findings of Espie in Central Otago (1994). It is a well-known phenomenon that fewer seedlings survive at higher densities (Harper 1977). Turkington and Harper (1979) found that germination and establishment of *Trifolium repens* seedlings in living swards was strongly suppressed

compared to seed which was sown in dead swards. Also, Lee, Fenner and Duncan (1993) found a halo around *Chionochloa rigida* where seedling establishment was rare. They suggested that this area was unfavourable for establishment due to canopy shading and root competition. This may partially explain the lack of seedlings found in this study. While the density of *H. pilosella* is locally high, there are areas of bare ground. The lack of seedling establishment in these areas may be due to unfavourable environmental conditions such as drought, frost, or nutrient depletion of the soil (either by *H. pilosella* depleting the soil of nutrients over long periods of time or from nutrient uptake by neighbouring plant roots over shorter periods of time).

The mean rainfall for the period of this study was over 25% higher than the 70-year average. The greatest increase was in two of the three spring months when inflorescence initiation occurred. This higher than average spring rainfall could have contributed to the overall cover increase in the control plots. In contrast, during the time that seedling establishment and daughter root formation would have taken place, December to February, the rainfall was considerably lower than average. It has been observed that during particularly wet years the occurrence of seedlings is greater (Bishop *et al.* 1978; Makepeace 1985b; Espie 1994) and drought has also been noted as a common cause of death among seedlings and daughters as well as rosettes. The drier, warmer summer may have played a part in the low numbers of seedlings seen in this study and may have adversely affected the population as a whole.

2.4.3 Cover

No other studies have looked at the effect of *H. pilosella* cover on its population dynamics at the rosette level. This study has shown that reproductive attributes of the population are more responsive to cover than to density. This may be due to the variation in plant size between treatments. Plant size was not measured between treatments, however it was noted that plants within fertilised and watered plots had a more lush appearance and grew larger leaves to the point where they lost their flat prostrate appearance (Figure 2.13). It may be that reproduction relates functionally to cover (via shading, local nutrient competition, etc.), and density does not directly relate to cover: high cover-plots may have fewer plants and vice versa.

With increased cover, mortality increased but there was also an increase in reproductive rates. This may be due to an increase in rosette size associated with high cover levels ($n = 30$, $p = 0.027$ for relationships between average subplot rosette diameter and % cover from control plot data). As indicated in Chapter 3, there is an effect of plant size on reproduction.

These responses to cover may also be a form of 'foraging' behaviour. Two types of foraging behaviour have been described; guerrilla and phalanx (Lovett Doust 1981). When resources are scarce, clonal species may take on a 'guerrilla' growth form by producing longer stolons to try and escape the situation. Clones in more favourable conditions may produce shorter stolons to efficiently exploit their environment (phalanx). Rosettes in higher-cover areas may be experiencing some adverse effect such as increased shading or competition for other resources. These rosettes are more likely to produce more stolons of longer length ensuring that their offspring have a better chance of establishing in the surrounding area where there may be less competition. This habit of 'choosing' sites with better growing conditions has been observed in other clonal species (Saltzman 1985; Pitelka & Ashmun 1986; Waller 1988; Wijesinghe & Hutchings 1997). At Mt. John, however, the reverse was observed. Under seemingly favourable conditions (additional water or fertiliser) *H. pilosella* rosettes produced longer stolons and had greater parent-to-daughter distance. Perhaps in this case it was not the water and nutrients which were limiting the population but space and light.

The initial cover of other species had no effect on the population dynamics of *H. pilosella*. This is not surprising as the area was dominated by *H. pilosella*. Also, both Watt (1981) and Kelly (1989) showed that in English grasslands *H. pilosella* influenced the distribution of less common species and Watt found that the reverse did not occur. If the effect of cover by other species had been followed for another year, there may have been different results. In the present study, there was a substantial increase in the cover of clover in plots which received additional water and this may have affected the reproductive and mortality rates of *H. pilosella* by increased competition for light. Indeed, other studies have suggested that there appears to be a tussock cover threshold above which *H. pilosella* has a competitive disadvantage (Foran *et al.* 1992) and that

cover of *H. pilosella* was lowest on areas where herbage was allowed to accumulate (Espie 1994).

2.4.4 Treatments

This study showed a difference in mortality between the control and treatment plots. All treatments (except fungicide/insecticide) caused a decline in plant density while the unamended plots had a slight increase. Similar results were obtained with the addition of nutrients in the Breckland plots (Davy & Bishop 1984) and with fertiliser treatments in New Zealand pastures (Scott *et al.* 1990a & 1990b). There are two explanations for the decline in the *H. pilosella* populations in the treatment plots. The first may lie in the demographic responses of the plants to increased moisture and nutrients. The proportion of daughters initiating an inflorescence increased 5-fold with the addition of water and fertiliser and there was a 100% increase in rosette inflorescence initiation. The flowering response of *H. pilosella* to nutrients has been observed elsewhere: Lloyd and Pigott (1967) found more than a fifty-fold increase in the number of inflorescences and Davy and Bishop (1984) found a five-fold increase in the probability of rosettes initiating inflorescences. This trend at Mt. John was apparent with or without the addition of the cutting treatment. While sampling did not occur during the second year, the continued effects of water and fertiliser on reproduction in the plots was apparent. During the reproductive period, flowering and growth within plots was easily recognisable as squares of bright yellow and green amid a grey and brown background.

The repercussions of such an increase in flowering are far reaching. It would result in increased stolon and daughter production and, because mortality and reproduction are so tightly linked, it would lead to higher rosette turnover. Daughter rosettes and seedlings would have had less chance of establishing due to the higher cover associated with the addition of nutrients. A higher proportion of daughters emigrated from the vicinity of their parent rosette due to increased stolon length and it is unlikely that there would have been enough recruitment to replace those rosettes lost to reproduction.

A second explanation for the decline of *H. pilosella* densities in the treatment plots may be the effect of both interspecific and intraspecific competition. The change in the visual appearance of the treatment plots was striking. Those plots which were given extra water

and nutrients had a lush green appearance as compared to those which did not and rosettes increased in size. Rosettes in these plots responded to the treatments by increasing their production of stolons and daughters and became so crowded that it was impossible to distinguish one rosette from another. Increases in rosette size have also been found in other studies (Davy & Bishop 1984; Svavarsdóttir 1995). In the absence of other species, there presumably would have been intensified intraspecific competition between roots, although this would have been reduced with additional water and fertiliser, and it is likely that smaller rosettes would have been shaded out by more vigorous rosettes. In addition, a decrease in the vigour of some rosettes may have been the result of allelopathic chemicals as suggested in a number of studies (Widera 1978; Davy & Bishop 1984; Makepeace *et al.* 1985; Fornasari 1996). This, combined with competition for nutrients or light, may have caused the demise of some of the population.

One of the most striking features that occurred during the study was the influx of *T. repens* observed in the water (especially) and fertiliser treatments during the second year. The mortality of *H. pilosella* rosettes and daughters within these quadrats increased but rosette reproduction increased only under the fertiliser treatment. Hence, with the addition of water, the increase in mortality can not be attributed to reproduction alone. Clover tended to grow over the *H. pilosella* rosettes which would have caused increased shading. *H. pilosella* has higher light requirements (Makepeace 1985b) and shading may have contributed to the greater decline in the population density of these plots compared with others. Davy and Bishop (1984) suggested that the decline in their Breckland plots was due to the shading out of *H. pilosella* by dense, tall stands of grasses which produce a substantial proportion of dead material. In addition, an increase in nutrients has been responsible for an increase in the competitive ability against *H. pilosella* of other species in other studies (Davy & Bishop 1984; Scott *et al.* 1990a & 1990b).

In their native habitat, *Hieracium* species never pose problems as weeds (Fornasari 1996), whereas in non-native habitats they are good competitors (Bishop & Davy 1994). Watt (1962) described the transition in Breckland from *Festuca ovina* to *H. pilosella* over a period of 25 years. This pattern occurred in both enclosed and grazed plots although the transition was slower in the presence of grazing. The invasion by *H. pilosella* was followed by its rapid spread and then its senescence and degeneration leading to the

exposure of bare soil and erosion. In the enclosed plot this was followed by a brief re-invasion of *F. ovina*. In a follow up study, Watt (1981) determined a third transition from *H. pilosella* to *Thymus* in both enclosed and control plots. A similar situation of the eventual replacement of *H. pilosella* by another species may occur in New Zealand in the future and is something that should be further considered. Certainly we have seen the first two parts of the pattern in New Zealand with the replacement of our tussock lands with *H. pilosella* and then the marked degradation of the *H. pilosella* infested areas (Treskonova 1991a & 1991b).

While water and fertiliser had marked effects on the vital rates of the Mt. John population, the same cannot be said for the cutting or fungicide treatments. The only effect cutting had was to decrease the success of flowering in rosettes and increase the proportion of rosettes initiating stolons. Similarly, Makepeace (1980) found an increase in stolon production in a cutting trial and Bishop and Davy (1984) detected an increase in stoloniferous daughters in the presence of grazing by rabbits. Other studies observed that when rabbits were excluded from plots, flowering of *H. pilosella* was the first noticeable response (Watt 1962; Bishop *et al.* 1978; Bishop & Davy 1984). Bishop and Davy (1984) suggested that this effect was due to the preferential grazing by rabbits on the developing buds. When they investigated the initiation of flowering they discovered the opposite; inflorescence initiation decreased in the absence of grazing by rabbits. They suggest that this is due in part to competition for resources diminishing the proportion of rosettes able to attain the critical size for flowering. In this study, while the effect was insignificant, inflorescence initiation increased slightly under the cutting treatment showing some consistency with Bishop and Davy. Espie (1994) found that in the presence of grazing there was no change in rosette number but there was an increase in % cover suggesting that rosettes increased in size, while Scott *et al.* (1990a) showed that grazing did little to change *H. pilosella* abundance. The present study was consistent with Scott *et al.* (1990a) in finding no effect on the change in density or cover in the cutting treatment.

2.5 Conclusions

The present study was the first to find density-dependent regulation of *Hieracium pilosella* populations in New Zealand, although this was implicit in some of Makepeace's

results. The population of *H. pilosella* at Mt. John was regulated by density-dependent mortality, rather than the density-dependent reproduction found in previous plant population studies. Moreover, about half of the *H. pilosella* mortality was not associated with reproduction. The Mt. John population appeared to be at or near an equilibrium at a density of ca 3200 rosettes/m², due to density-dependent rosette mortality interacting with density-independent reproduction. This apparent stability may be subject to a longer-term trend due to plant-induced environmental degradation operating on a time-scale of decades. Such a possibility is suggested by the presence of substantial bare ground, the lack of obvious discrete patches of *H. pilosella*, and the low reproductive rates compared with earlier estimates, combined with anecdotal evidence that *H. pilosella* has been present for more than thirty years. However, the nature of this degradation remains unknown.

The effects of additional fertiliser and/or water on the population were apparent in the first year. There was a decrease in the overall density of *H. pilosella* in the treatment plots whereas density in the control plots remained constant. While the overall cover increased in the treatment plots, the continued decline in density could be followed eventually by a decline in cover, especially if other species are able to better compete with *H. pilosella*.

Simulated grazing had little effect on the Mt. John *H. pilosella* population, suggesting that the removal of grazing animals would do little to control the population or its spread, at least in the short term. In the longer term, the removal of disturbance by herbivorous mammals may allow other plant species to become established and replace the current *H. pilosella* population, as happened in Breckland (Watt 1981). Unfortunately, any such changes are likely to be extremely slow and correspondingly difficult to study.

3. Age and Size distribution in *Hieracium pilosella*

3.1 Introduction

The effects of age, size and nearest neighbour distances (or density) on plant reproduction have been studied in many plant species. For example, Baskin and Baskin (1979) showed that the probability of flowering increased with size in the monocarpic perennial *Pastinaca sativa*, while Leverich and Levin (1979) found age to be important in *Phlox drummondii*. Other studies suggest that while there is a reproductive size threshold, density may play a part in the plants' ability to reach the critical size for flowering (Werner 1975; Harper 1977; Weiner 1988).

In *Hieracium pilosella* Widera (1978) observed that size, measured as rosette diameter, decreased with increasing density and also that size corresponded to age. In their Breckland study, Bishop, Davy and Jefferies (1978) discovered that rosettes less than 2 years old reproduced more than those older than 2 years. The 1 - 2 year old group had the greatest proportion reproducing. Bishop and Davy (1985) suggested that there was a size threshold for inflorescence and stolon initiation based on a correlation between density and reproduction, but did not quantify their hypothesis.

The first year of observations of *H. pilosella* inflorescence and stolon production at Mt. John suggested there might be a relationship between reproduction and size or age of rosettes. These observations were quantified in 1995/96 by expanding the control and fungicide/insecticide treatment initiated in 1994 (Chapter 2) to include rosette size measurements, and also to divide the population into age groups. These two treatments were most similar to the general population on unimproved land and did not include the changed population dynamics of the water, fertiliser or cutting treatments.

3.2 Methods

3.2.1 Experimental design

The study used the four control and fungicide/insecticide plots established during the first year of the study. The plots are described fully in the methods section of Chapter 2.

For each rosette in the original quadrats, inflorescence initiation, stolon and daughter production, distance to nearest neighbour rosette, longest leaf length and rosette diameter

were recorded. Nearest neighbour distance was measured as the smallest distance between rosette leaves of neighbouring plants and longest leaf length was measured from the central growing region of the rosette to the end of the longest leaf. Rosette diameter was measured as the largest diameter through the centre of the rosette. These measurements were taken approximately bi-monthly between October 1995 and April 1996.

Reproductive rosettes were defined to be those rosettes which initiated inflorescences. These rosettes might or might not have produced stolons and/or daughter rosettes.

3.2.2 Statistical analysis

To test whether reproduction was affected by age, rosettes were separated into two age classes; those one year old or less, and those older than one year. The fraction of rosettes which were reproductive in each plot and age class was determined. A t-test was then carried out the four log ratios of reproductive proportions in the two age-classes to determine if the ratio was significantly different from 1 (i.e. the log ratio significantly different from 0).

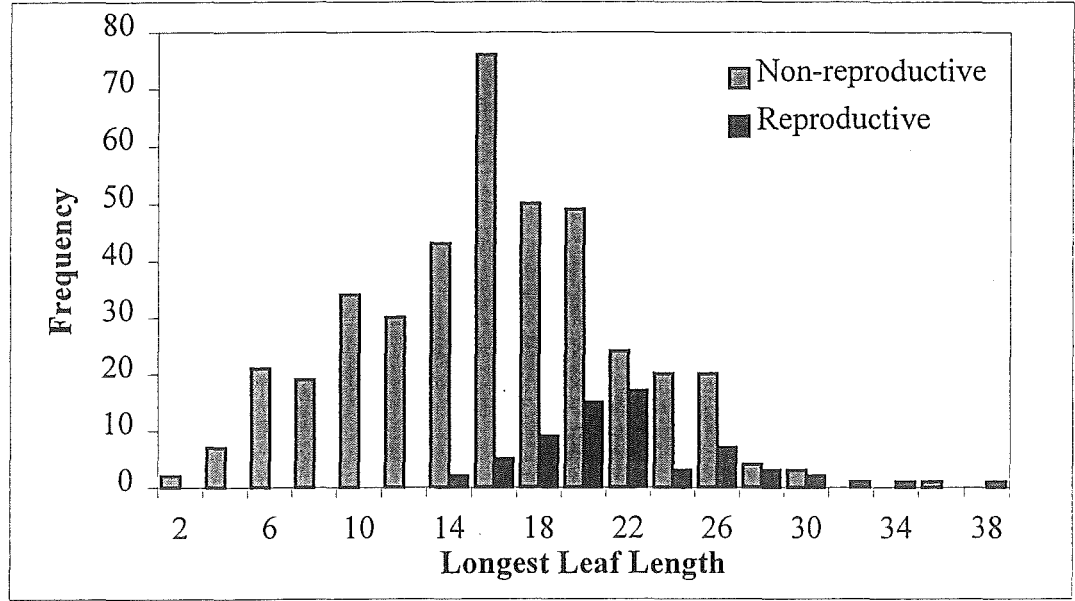
To test for relationships between reproduction and rosette size or nearest neighbour distance, the rosette data from the plots were sorted into reproductive and non-reproductive groups. The average size (measured as longest leaf length or diameter) and nearest neighbour distance were then calculated for each group, resulting in 8 groups, two for each plot. Because several measurements were taken during the course of the study, the largest size measurement and smallest neighbour distance for each rosette were used. Size and distance relationships were then analysed using an analysis of variance with reproduction a factor with two levels (reproduced or not) and plot as a block effect.

Analysis of covariance was used to determine if there was a relationship between plant size and density with plot as a treatment factor and density as the covariate. All analyses used Genstat 5 (Genstat 5 Committee 1993).

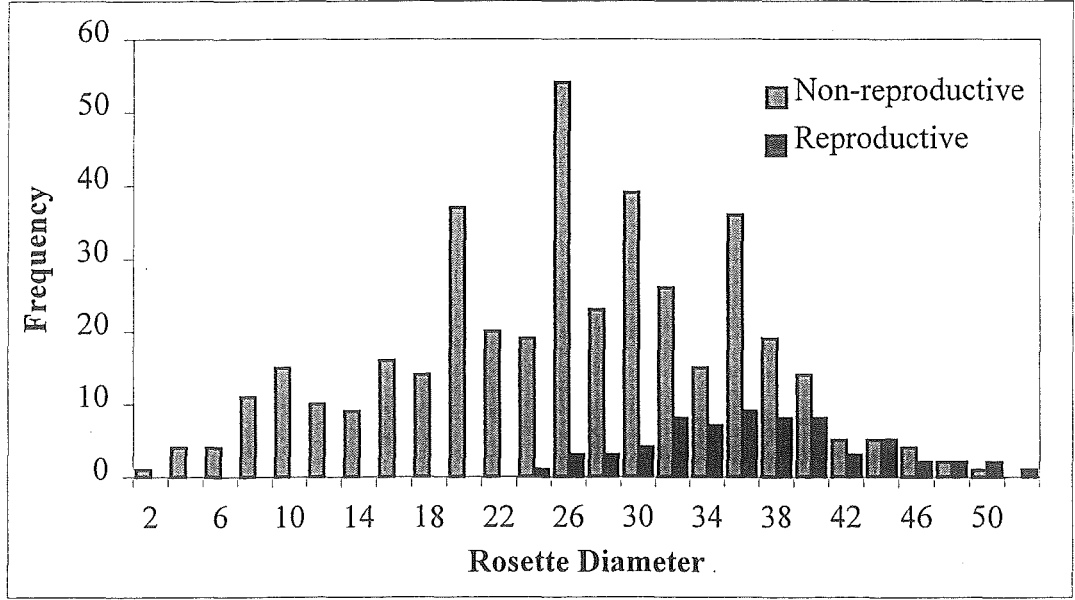
3.3 Results

The frequency of reproductive and non reproductive plants for different rosette sizes is shown in Figure 3.1. Rosettes did not reproduce until their longest leaf lengths were at

least 13 mm or their diameters were at least 23 mm. Most reproduced at longest leaf lengths greater than 18 mm or diameters greater than 30 mm. The relationship between size and reproduction was statistically significant for both diameter ($p = 0.013$) and longest leaf length ($p < 0.001$) (Table 3.1).



(a) Rosette size measured as longest leaf length (mm).



(b) Rosette size measured as rosette diameter (mm).

Figure 3.1 Frequency of reproduction based on the size of *Hieracium pilosella* rosettes from the field study at Mt. John, Lake Tekapo.

Table 3.1 ANOVAs of size and reproduction for *Hieracium pilosella*. * $p < 0.05$, *** $p < 0.001$

Source of Variation	df	Diameter		Longest leaf length	
		MS	F	MS	F
Block	3	14.54	2.24	3.07	154.79
Reproduction	1	130.25	20.06 *	56.27	2835.36 ***
Residual	3	6.49		0.02	
Total	7				

In all plots, the ratio of reproductive to non-reproductive plants was greater in the younger age class, with the overall difference being significant: an average of 50% reproduced in the ≤ 1 year age class and 11% reproduced in the > 1 year age class (Table 3.2).

Table 3.2 % of *Hieracium pilosella* rosettes reproductive in each age group for each of 4 plots. * $p < 0.05$

Plot	Age Class		t-test (df = 3)
	≤ 1 Year	> 1 Year	
1	20	10	
2	52	7	
3	42	13	
4	82	13	
Overall	50	11	4.87 *

There was no significant relationship between reproduction and nearest neighbour distance ($F = 0.02$ and $p = 0.895$; Table 3.3), or between plant size and density ($F = 0.16$ and $p = 0.691$ for diameter and $F = 0.71$ and $p = 0.407$ for longest leaf length).

Table 3.3 Mean (\pm SD) nearest neighbour distance (mm) for reproductive and non-reproductive *Hieracium pilosella* rosettes.

Plot	Reproductive	Non-reproductive
1	9.7 \pm 6.5	9.5 \pm 4.2
2	10.1 \pm 5.3	11.8 \pm 6.9
3	9.9 \pm 5.3	9.3 \pm 4.3
4	11.4 \pm 4.5	10.4 \pm 6.1

When different-aged plants were matched for size (Table 3.4), young plants were more likely to initiate inflorescences at all sizes above the minimum for flowering (except for two comparisons with small sample sizes). There was no evidence for a smaller size threshold in younger plants nor a relationship between size and age (Table 3.5).

Table 3.4 Percentage of *Hieracium pilosella* rosettes initiating inflorescences by age and size (longest leaf length or diameter). Total number of rosettes in each category is given in parentheses. “---” signifies there were no plants of that size and age.

Size class (mm)	Percentage reproducing (n)			
	Longest leaf length		Diameter	
	≤ 1 Year	> 1 Year	≤ 1 Year	> 1 Year
0 - 10	0 (31)	0 (53)	0 (14)	0 (15)
11 - 20	16 (91)	9 (233)	0 (39)	4 (71)
21 - 30	64 (25)	33 (55)	18 (39)	8 (153)
31 - 40	0 (1)	100 (1)	42 (48)	22 (85)
41 - 50	---	---	57 (7)	25 (16)
51 - 60	---	---	100 (1)	50 (2)

Table 3.5 Mean (± SD) longest leaf length (mm) and diameter (mm) for *Hieracium pilosella* rosettes in two age classes.

Plot	Longest leaf length		Diameter	
	≤ 1 Year	> 1 Year	≤ 1 Year	> 1 Year
1	14.3 ± 6.9	14.7 ± 5.5	21.6 ± 10.6	22.7 ± 7.9
2	15.0 ± 4.8	14.8 ± 4.5	25.1 ± 9.3	24.9 ± 8.3
3	16.4 ± 5.2	17.8 ± 4.3	30.0 ± 9.7	31.8 ± 7.3
4	14.4 ± 6.9	16.0 ± 5.5	21.5 ± 11.1	24.8 ± 8.4

3.4 Discussion

Both size and age were found to be important in the inflorescence initiation of *Hieracium pilosella*. A minimum size threshold of 23 mm diameter (13 mm longest leaf length) had to be achieved before any rosettes reproduced. This finding supports Bishop’s and Davy’s (1985) suggestion that a size threshold exists for inflorescence initiation in *H. pilosella*.

Several authors have shown that size thresholds exist for flowering in monocarpic perennials or facultative biennials (in the sense of Kelly 1985) (Table 3.6). In studies on facultative biennial plants, Werner (1975) and Gross (1981) found that a minimum size was required before plants initiated inflorescences and that the probability of flowering increased with increased rosette size. In a clonal monocarpic perennial, van der Meijden and van der Waals-Kooi (1979) showed that not only was there a size threshold for flower initiation in *Senecio jacobaea* but that the number of vegetative ramets increased with parent plant diameter. In many of these studies the authors suggest that the strategy of smaller plants in a population to “switch” from strict biennials to facultative biennials allows them to accumulate sufficient resources for reproduction. In addition, van der Meijden and van der Waals-Kooi (1979) suggested that by delaying flowering, smaller plants may grow to a larger size in the next season and produce more seed than they would have done in the previous year.

In another study of non-monocarpic *Viola* species Thompson and Beattie (1981) demonstrated that a size threshold in the form of weight existed for both seed and stolon production and that the size of plants was inversely related to plant density. They suggested that decreased flowering and stolon production at higher densities was due to a decrease in plant biomass caused by increased competition for limited resources. This view was echoed by Bishop and Davy (1985) for *H. pilosella*. The population of *H. pilosella* at Mt. John, however, showed no relationship between reproductive effort and density (Chapter 2) nor size and density. The lack of an effect of density at Mt. John may be because average plot density or nearest neighbour distance is a poor measure of density for individual plants. If competition is mainly below ground or plant size varies widely, a large neighbour further away could have a greater effect than a small neighbour close by. In their glasshouse study Bishop and Davy (1985) found that even at the highest density used, where 74% of the rosettes produced no stolons, three rosettes produced 8 or more stolons each. They suggest that this inequality of stolon production reflects an hierarchical structure of dominant and suppressed rosettes. Another explanation may be that fine-scale spatial soil variation makes local density an inappropriate measure of plant resources.

Table 3.6 Some facultative biennial plant species where size thresholds for reproduction have been shown.

Species	Size measure	Source
<i>Carduus nutans</i>	rosette diameter; rosette area	Lee & Hamrick, 1983 ; Shea, 1994 ; Shea & Kelly, in press
<i>Carex bigelowii</i>	number of green leaves	Carlsson & Callaghan, 1990
<i>Carlina vulgaris</i>	mass measured as diameter \times number of leaves	Klinkhamer <i>et al.</i> , 1996
<i>Daucus carota</i>	root crown diameter	Gross, 1981
<i>Dipsacus fullonum</i>	rosette diameter	Werner, 1975
<i>Erigeron strigosus</i>	dry weight	Hirose & Kachi, 1982
<i>Oenothera biennis</i>	rosette diameter	Gross, 1981
<i>Oenothera erythrosepala</i>	dry weight	Hirose & Kachi, 1982
<i>Pastinaca sativa</i>	root crown diameter	Baskin & Baskin, 1979
<i>Senecio jacobaea</i>	rosette diameter	van der Meijden & van der Waals-Kooi, 1979
<i>Tragopogon dubius</i>	root crown diameter	Gross, 1981
<i>Tragopogon pratensis</i>	root crown diameter	Qi <i>et al.</i> , 1996
<i>Verbascum thapsus</i>	rosette diameter	Gross, 1981

Rees and Crawley (1989) contest the idea of reproductive thresholds, suggesting that, because of their modular construction, plants are less likely than animals to display size thresholds for reproduction. They argue that, because animals' development is determinate and the life-cycle consists of a number of discrete phases, one would expect them to have significant reproductive thresholds whereas development in plants consists of repeated iterations of similar construction. In a rebuttal, Silvertown (1991) pointed out that virtually every semelparous perennial plant studied has a size threshold for reproduction and that most perennial plants must reach a minimum size before they reproduce. Based on results of this and other studies, it is difficult to ignore the existence of reproductive thresholds in plants. However, Rees and Crawley (1989) may be partly right in that the size thresholds are often quite low for plants and have much less effect on plant population dynamics than occurs amongst animal species.

The association between age and reproduction in herbaceous perennial or facultative biennial plants is less well documented, because of the plasticity of plant growth in response to different environmental stresses and, more particularly, the difficulty in determining plants' ages once past the seedling stage in most herbaceous species. There have, however, been a few studies which have either endeavoured to follow herbaceous plants from their emergence as seedlings to their death (Werner 1975; Leverich & Levin 1979; Gross 1981; Lee & Hamrick 1983) or have determined the approximate age of individuals in a population over the course of a several year study (Bishop *et al.* 1978). In a study of *Phlox drummondii*, Leverich and Levin (1979) derived age-specific life tables for *P. drummondii* and observed that the reproductive value verses age curve was similar to that for animals. In addition, the contribution of larger individuals was greater than that of smaller individuals over all ages. Both Werner (1975) and Gross (1981) compared age and size as predictors of fate in facultative biennial species and concluded that while age had some effect on flowering in a given size category, size was a much better predictor; in all species studied, the probability of flowering increased with plant size. In a field study of *Carduus nutans*, Lee and Hamrick (1983) came to the same conclusion as Werner and Gross: while flowering and seed production of individual plants was significantly correlated with both age and size, size was the better predictor. This finding was also confirmed by Shea and Kelly (in press).

For *H. pilosella* in Breckland, UK, Bishop *et al.* (1978) were able to divide the population into four age groups: < 1 year old; 1 year old; 1 - 2 years old; and > 2 years old. They found that a higher proportion of rosettes initiated inflorescences in their first two years with the highest proportion occurring in the 1 - 2 year age group. In the present study at Mt. John, an average of 50% of rosettes one year of age or less reproduced whereas an average of only 11% of the older rosettes reproduced. Since size and age seemed to be unrelated, it may be possible that age is acting secondarily to size in determining the reproductive fate of rosettes. There are several ways which this might happen. Firstly, there may be an inherent physiological effect of age on reproduction. Secondly, the effect may be microsite-related: daughter rosettes may be in a better position at the microsite level thus allowing them access to additional resources such as nutrients or water. Based on the data collected in this study it would be difficult to prove or disprove this theory but, because of the apparently degraded nature of the Mt. John site, this is an unlikely explanation.

Another possible explanation for increased reproduction in younger rosettes may be due to young daughter rosettes receiving extra nutrients from the parent rosette via the stolon. Nobel (1987) suggests that the precocious formation of inflorescences in ramets of *Agave deserti*, which otherwise would have been too small and young to flower, was due to the movement of hormones from the parent to daughter plant via the rhizome and that the movement of water through the stolon was important at the juvenile stage. In addition, Slade and Hutchings (1987) showed that the sizes of newly established clones of *Glechoma hederacea* were larger when parents were in nutrient-rich areas suggesting that the movement of nutrients along the stolon was important in the ramets' growth.

The timing of daughter production may also be important in determining whether a young rosette will reproduce in its first year. Daughter rosettes produced early in the season have more time to grow and accumulate reserves necessary for reproduction whereas rosettes produced later in the summer might be unable to reach this critical size before the onset of winter. This was found to be the case in *Carex bigelowii* (Carlsson & Callaghan 1990). Carlsson and Callaghan observed that the probability with which a tiller undergoes floral initiation depended on size and the time it emerged. They

suggested that shoots emerging earlier in the season would have the opportunity of a longer growing period and could be more heavily supported by the parent.

Classical demographic models developed for animal populations in the 1940s and 1950s were defined by a specific set of age-dependent vital rates (e.g. Leslie & Ransom 1940; Leslie 1945; Deevey 1947). Because life cycles of most plants violate the assumptions of these earlier demographic models, vital rates written as functions of age are generally poor predictors. More recently, however, these classical models have been extended to include stage-dependent vital rates (Caswell 1986). Werner and Caswell (1977) developed both age and size distribution models for teasel (*Dipsacus fullonum*) and found that models based on size gave more satisfactory results. This view was confirmed by Thompson and Beattie (1981) for 2 *Viola* species and Gross (1981) for 4 facultative biennial species. All authors concluded that because of the plastic nature of growth in plants it is difficult to accurately age herbaceous individuals.

When both age and size can be determined, there may be merit in incorporating both into a model. Meagher (1982) developed a model based on size classes for the perennial *Chamaelirium luteum* but noted that there were also age components that came into effect. In an earlier study of *C. luteum* Meagher and Antonovics (1982) found that, among juvenile plants, the largest had lower mortality rates and higher reproductive values and when sensitivity analyses were run on the size structured model, the population was most strongly influenced by juvenile characteristics, especially age at first reproduction (Meagher 1982). Gross (1981) also suggested that while the size structure of a plant population is a better predictor than age, the age structure of a population may also be important in determining the populations behaviour, especially in species where mortality remains high for individuals above the minimum size for flowering. Certainly in the case of *H. pilosella* both age and size would be useful indicators of reproductive probabilities, although the age dynamics of a population would need to be studied further; it is not known what role age plays in the non-reproductive mortality of rosettes, especially in older individuals.

3.5 Conclusions

The data presented here suggest a strong link between reproduction and both plant size and age in *Hieracium pilosella*. The effect of age found in this study seems to be stronger than in the few previous studies of other herbaceous species, so could be worth further investigation to determine the mechanisms responsible; those involved in determining reproductive activity after rosettes have reached the minimum size for inflorescence initiation are not well understood. It seems likely that nutrient supply may play an important role in the process, especially in view of the high proportion of young rosettes which reproduce; rosettes which can capture enough resources are better able to reach the critical size for reproduction. Interestingly there seemed to be no change in threshold size with respect to age, only in the probability of flowering at a given size over the threshold.

The relationship between plant size and reproduction has the practical merit that size is easily measured whereas determining the age structure of a population is difficult in most herbaceous species. The classical age-structured demographic models can then be easily applied by modifying them to stage- (size-) structured models. However, the effect of age within each stage or size class may also be important in determining the behaviour of a population.

4. Soil and Site Comparison

4.1 Introduction

Several researchers have suggested that *Hieracium pilosella* changes its soil environment, providing a competitive advantage over other resident species (Widera 1978; Davy & Bishop 1984; Makepeace *et al.* 1985; McIntosh *et al.* 1995; Espie & Boswell unpublished manuscript). However, over time, this process is not only detrimental to competitive species but also to *H. pilosella* itself. Widera (1978) and Makepeace, Dobson and Scott (1985) showed that the allelopathic chemical umbelliferone found in *H. pilosella* inhibited the germination of seedlings of several species including *H. pilosella*, while Guyot (cited in Widera 1978) suggested that auto-intoxication took place, resulting in the formation of bare regions in older *H. pilosella* patches. Henn, Petit and Vernet (1988), however, suggested that the lack of evidence of allelochemicals in field soils meant that *H. pilosella* did not conform to the definition of an allelopathic species.

Scott (1975) and McIntosh and Allen (1993) showed that soils under *H. pilosella* patches were more acidic than soils found under most other nearby resident species. This was confirmed by McIntosh *et al.* (1995), who also demonstrated a difference in levels of organic carbon, calcium and magnesium in soils under *H. pilosella* and non-*H. pilosella* areas. In a recent study, Espie and Boswell (unpublished manuscript) suggested that higher soluble aluminium levels under *H. pilosella* plants, associated with high acidity, may assist in the plants' ability to displace other species as well as the demise of itself. Both McIntosh *et al.* (1995) and Espie and Boswell (unpublished manuscript) found that exchangeable calcium, magnesium, and potassium were lower in the halo regions (i.e. bare areas around patches) and higher in the central regions of *H. pilosella* patches.

In glasshouse competition trials, researchers have shown that *H. pilosella* was able to reduce the growth of *Festuca novae-zelandiae* (Makepeace *et al.* 1985; Svavarsdóttir 1995; Fan & Harris 1996) and that this reduction in growth was dependent on fertility, with *H. pilosella* being more aggressive with added phosphorus (Svavarsdóttir 1995). However, in the field, the addition of nutrients resulted in the suppression of *H. pilosella* due to increased competition from other species (Davy & Bishop 1984).

Reproductive output has been shown to increase with added nutrients in both the glasshouse and field. Svavarsdóttir (1995) found an increase in both inflorescence and stolon production, as did Fan and Harris (1996). In the field, Davy and Bishop (1984) discovered that a higher proportion of plants produced flower stalks when nutrients were added. At Mt. John added fertiliser increased the proportion of rosettes producing stolons and inflorescences as well as increasing stolon length and average daughter number per rosette (Chapter 2).

Given the evidence that *H. pilosella* changes its soil environment in some way, it is important to know how these changes affect the population itself in the absence of competition and soil amendment. The purpose of this study was to determine if soils having a different history of *H. pilosella* growth cause differences in plant vigour and, if so, to quantify these differences. To this end, a glasshouse experiment was carried out to compare growth and reproductive rates of single plants, assumed to be genetically similar, grown in unamended soil cores from two different sites in the field, in the absence of competition for light, water or space.

4.2 Methods

4.2.1 Site characteristics

The two sites chosen for soil cores were Mt. John, Lake Tekapo and Port Levy Saddle (43° 43'S, 172° 46'E) on the Banks Peninsula, Canterbury. The Mt. John site is described in Chapter 2 of this thesis; it has had dense stands of *Hieracium pilosella* for at least 3 decades, and the vegetation is primarily *H. pilosella* with grasses and other herbs interspersed by bare ground. Port Levy is 690 m in altitude and receives approximately 1800 mm rainfall annually. The site was grazed by cattle from 1961 - 1985 (December - June each year). Since then it has been lightly grazed all year by sheep, with summer grazing by cattle during the last few years (G. Young, *pers. comm.*). *H. pilosella* occurs in occasional distinct patches of up to 3 m in diameter surrounded by pasture grasses on the flat summit of the saddle and is absent on the steeper slopes below. *H. pilosella* has occurred there for at least 30 years in approximately the same position (G. Young, *pers. comm.*).

4.2.2 Experimental design

The experiment used a split plot design with main plots corresponding to 13 *H. pilosella* patches from each of the two sites. For each patch, four intact soil cores were removed, two from the centre and two from the area outside the patch where *H. pilosella* was absent and likely to not be having any effect (usually 1m away), resulting in a total of 104 cores. The main plot treatment factor was site (Mt. John or Port Levy) and the subplot treatment factor was patch position (centre or outside). The cores were 6.5 cm in diameter and 4.5 cm in depth. All original vegetation within the cores was removed using tweezers to minimise soil disturbance. In addition, smaller soil samples were collected from the side of each core hole for pH tests. All soil cores and samples were collected on 1 - 4 November, 1996.

The smaller soil samples were air dried and sieved to <2 mm. pH was measured using a 1:5 soil to distilled water ratio. Two pH standards were used to calibrate the pH meter; pH 4.0 and 7.0. An amount of soil similar to the samples was used as a standard to check the consistency of pH results over time. Duplicate sub-samples of this “quality control” soil sample were run with each batch of samples measured. Failure of the control soil sample to fall within acceptable limits (± 0.05 pH units) resulted in the whole batch of samples being reanalysed. The remaining soil was stored under dry conditions in case further soil samples were required.

H. pilosella plants were collected at Mt. John on 4 November, 1996 by removing a 50 × 50 cm square of soil to a depth of approximately 20 cm from a single group of rosettes. The sample was well watered, covered in plastic to reduce evaporation and taken back to the glasshouse within 24 hours of being removed. Individual rosettes were separated out from the soil and rinsed to remove remaining soil. Prior to planting the wet weight, longest leaf length and diameter of each rosette was recorded. Wet weight was recorded to the nearest 0.01 g and leaf and diameter measurements were made with electronic callipers to the nearest 0.01 mm. A single rosette was planted in the centre of each core on November 5, 1996. Because the plants came from one patch and were likely a single clonal colony, it was assumed that they were of a single genotype.

After planting, the cores were placed in a glasshouse at AgResearch, Lincoln. Air temperature in the glasshouse was generally in the range of 18-26 °C over the period of

the experiment. Each core had an individual drainage tray to prohibit the uptake of any leachate from other cores (Figure 4.1). The plants were watered three times a week and inflorescence, stolon and daughter production were recorded weekly between November 1996 and September 1997. Any other vegetation which appeared in the pots over the period of the experiment was removed. After approximately one month from the initial removal of vegetation within the cores, the number of other plants appearing greatly decreased. In March, some of the plants showed signs of a root fungus so all plants were sprayed with a fungicide (Captan). After one treatment the fungus was controlled and no further spraying was required.



Figure 4.1 Soil cores and *Hieracium pilosella* plants during the glasshouse experiment. Each core had an individual drainage tray to prohibit the uptake of any leachate from other cores.

In September 1997, the longest leaf length, rosette diameter and stolon length were again measured before the plants were removed from their pots. Once removed, the rosettes were washed free of soil by immersing in water and using fine water spray, and the final wet weight was recorded. Roots, shoots, stolons and daughter rosettes were separated for each core and dried at 80 °C until a constant weight was achieved. Dry weights were measured to ± 0.01 g.

In October 1997 initial analysis of the data indicated that further soil sample analysis was needed. The original soil samples from Mt. John and Port Levy were randomly bulked

for each site and patch position to obtain a total of 16 soil samples, 4 for each site/patch position. The samples were analysed for basic soil nutrients including calcium (Ca), phosphorus (P), potassium (K), magnesium (mg), sodium (Na), and sulphur (S) as well as pH, total nitrogen (TN), and soluble aluminium (Al) using standard tests conducted by AgResearch Soil Testing Laboratories at Invermay.

4.2.3 Statistical analysis

It is usual to analyse data from a split-plot design using Analysis of Variance (ANOVA), however, death of rosettes due to reproduction during the course of the experiment resulted in unbalanced treatment numbers for wet and dry weight analyses. To analyse the data by ANOVA a balanced design is required. One way to create a balanced design is to approximate the missing values by using the mean of the non-missing treatment values. An alternative is to use a Generalised Linear Model (GLM) in which data can be analysed and interpreted in a similar way to an ANOVA (Zar 1996). Data were initially analysed using both methods. In both cases the results were the same, so only the GLM analysis will be reported here.

Analysis was performed using Genstat 5 (Genstat 5 Committee 1993). With the exception of number of daughter rosettes produced, number of stolons, inflorescence initiation and pH, data were first transformed by using the log of the pair average for each patch centre and outside. Pair averages were used to uphold the assumption of independent samples in the GLM procedure. Once transformed, the GLM analysis was carried out using a normal distribution with the identity link function which relates the explanatory variables to the mean of the response variable (Genstat 5 Committee 1993).

For the number of daughters and stolons produced, the numbers were totalled over both replicate cores from each patch. For example, if the plant in centre core A from Mt. John patch 1 produced two daughters and that in centre core B from the same patch produced 3 daughters, a total of 5 daughters would have been produced from that pair of plants. These data were then analysed using the Poisson distribution with a log link function.

The data for inflorescence initiation were binomial; either a rosette initiated an inflorescence or did not. To analyse these data, the number of “successes” was tallied for

each centre- and outside-patch pair, with success being defined as initiating an inflorescence. The data were then analysed using the binomial distribution with a logit link function as the number of successes out of 2.

In some cases, the means of the treatments suggested a position (outside vs. interior) effect in Port Levy but not Mt. John soils, though this was not significant in the GLM analysis. In these cases, GLMs were run separately for each site.

The bulked soil samples were analysed using ANOVA with site and position as factors and the different nutrients, soil pH or soluble aluminium, sampled as variates. To determine which if any of the sampled nutrients were related to reproductive effort (inflorescence initiation, daughters per rosette and stolon length) or growth rate (longest leaf length, rosette diameter and wet weight ratio), reproductive effort and growth rate averages were calculated for each of the bulked groups. Backward step-wise multiple regressions were then run using nutrients as predictors and average growth rates or reproductive averages as the response variate.

4.3 Results

4.3.1 Soil analysis

At both Mt. John and Port Levy, soils in the central region of *Hieracium pilosella* patches had lower soil pH with the soils at Port Levy having lower levels overall (Table 4.1). The differences between sites and positions were significant ($p < 0.001$ and $p = 0.002$ respectively).

Soluble aluminium levels were significantly lower at Mt. John than at Port Levy ($p < 0.001$) for both the central and outer patch regions and at both sites, the level of aluminium was higher in patch centres ($p = 0.023$).

Of the cations analysed (Table 4.1), potassium and magnesium were significantly lower ($p < 0.001$) and calcium was significantly higher ($p < 0.001$) at Mt. John than at Port Levy. With the exception of calcium at Port Levy, these cations were higher in the central region of patches than in the surrounding patch regions although this difference in position was only significant for potassium ($p = 0.011$).

Table 4.1 Means from soil analyses for soil cores from within and outside of *Hieracium pilosella* patches at Mt. John and Port Levy. All units are quick test units except total nitrogen (%) and pH (pH units).

	pH	P	K	Mg	Ca	Na	S	TN	Al
Mt. John centre	5.400	10.50	7.50	20.25	6.50	2.00	2.25	0.405	2.25
Mt. John outside	5.525	5.25	6.00	19.25	5.75	2.00	3.00	0.375	1.62
Port Levy centre	4.975	6.00	11.50	29.50	3.00	6.25	22.00	0.645	8.85
Port Levy outside	5.025	7.25	9.25	26.50	3.00	5.25	19.50	0.665	7.50

The effect of position on the amount of phosphorus and sulphur were opposite for the two sites. Phosphorus was higher in patch centres at Mt. John but lower in patch centres at Port Levy. There was no overall difference in the amount of phosphorus between the sites ($p = 0.054$) but there was for position ($p = 0.005$) and site \times position ($p < 0.001$). Sulphur was lower in soil from the central region of *H. pilosella* patches at Mt. John but higher at Port Levy. The differences in sulphur between sites and site \times position were significant ($p < 0.001$ and $p = 0.010$ respectively) but position on its own gave no significant difference ($p = 0.128$).

Total nitrogen was significantly lower at Mt. John ($p < 0.001$) than Port Levy but within each site the difference between positions was not significant. Sodium was also significantly lower at Mt. John than at Port Levy ($p < 0.001$).

When position was analysed separately for the two sites, only sodium and sulphur were significantly different in soil cores from Port Levy ($p = 0.030$ and $p = 0.040$ respectively). In both cases the elements were higher in soil from the centre of *H. pilosella* patches. At Mt. John, phosphorus was significantly higher in soil from the central patch region ($p < 0.001$) as was acidity (i.e. lower pH) and the amount of soluble aluminium ($p = 0.002$ and $p = 0.043$ respectively).

4.3.2 Reproduction

Reproductive attributes varied between sites and between patch position at Port Levy (Table 4.2, Table 4.3a - c). The plants grown in soil from outside *H. pilosella* patches at Port Levy had the highest rate of reproduction, with 50% of the rosettes initiating inflorescences compared to only 8% for rosettes grown in soil from Port Levy patch

centres and 12% - 15% for plants grown in Mt. John soil. The site effect on inflorescence initiation was not statistically significant whereas position was highly significant (Table 4.3a). This significance in position is mainly due to the large difference in inflorescence initiation between patch positions at the Port Levy site which explains the significant interaction term (Table 4.3a). When data were analysed for the two sites separately, position was significant for Port Levy but not Mt. John ($F = 18.91, p < 0.001$ and $F = 0.57, p = 0.464$ respectively).

Table 4.2 Percent of rosettes initiating inflorescence and treatment means \pm standard deviations for other reproductive attributes, with number of reproductive rosettes or stolons (out of 26 for each treatment) in parentheses, for *Hieracium pilosella* rosettes from Mt. John grown in soil cores from within and outside *H. pilosella* patches from Mt. John and Port Levy.

Site and position	Inflorescence initiation (%)	Daughters per reproductive rosette	Stolons per reproductive rosette	Average stolon length (mm)
Mt. John centre	12	2.0 \pm 0.0 (3)	2.3 \pm 0.6 (3)	23.7 \pm 22.2 (7)
Mt. John outside	15	2.3 \pm 0.5 (4)	2.0 \pm 0.0 (4)	17.9 \pm 24.3 (8)
Port Levy centre	8	3.0 \pm 1.4 (2)	2.0 \pm 2.8 (2)	41.3 \pm 24.5 (3)
Port Levy outside	50	3.3 \pm 1.6 (13)	3.5 \pm 1.6 (13)	82.5 \pm 68.0 (40)

The different sites only slightly affected the number of daughters and stolons produced by rosettes, with Port Levy producing more daughters and stolons per rosette pair (Table 4.3b and c). Position had the greatest effect on stolon and daughter number per rosette with the greatest numbers being produced by rosettes grown in soil from outside *H. pilosella* patches (Table 4.3b and c). As was the case for reproductive rosettes, the effect of position was mostly due to differences in stolon and daughter numbers between patch position at Port Levy. Separate analyses for the two sites showed no significant difference in number of stolons or daughters produced at Mt. John ($F = 0.8, p = 0.39$ and $F = 0.09, p = 0.764$ respectively) whereas differences at Port Levy were highly significant ($F = 21.14$ for stolons, $F = 27.15$ for daughters with $p < 0.001$ in both cases). Average length of stolons produced was also greater at Port Levy but statistical analysis was not possible due to the large number of rosettes which did not produce stolons (Table 4.2 and Figure 4.2).

Table 4.3 General Linear Model results for the reproductive attributes of *Hieracium pilosella* rosettes grown in soil cores from within and outside *H. pilosella* patches from Mt. John and Port Levy. *** $p < 0.001$, ** $p < 0.01$, * $p < 0.05$, ns = not significant.

(a) Inflorescence initiation per sample pair.

	d.f	s.s	F ratio
Site	1	3.759	3.13 ns
Mainplot error	24	28.760	
Position	1	11.691	19.02 ***
Site × Position	1	4.001	6.51 *
Subplot error	24	14.753	
Total	51	62.964	

(b) Number of daughter rosettes produced per sample pair.

	d.f	s.s	F ratio
Site	1	19.883	6.19 *
Mainplot error	24	76.968	
Position	1	31.004	27.80 ***
Site × Position	1	10.502	9.42 **
Subplot error	24	26.770	
Total	51	165.127	

(c) Number of stolons produced per sample pair.

	d.f	s.s	F ratio
Site	1	19.026	6.83 *
Mainplot error	24	67.010	
Position	1	26.954	23.98 ***
Site × Position	1	5.146	4.58 *
Subplot error	24	26.977	
Total	51	145.113	



Figure 4.2 Difference in *Hieracium pilosella* stolon length between patch position (centre and outside) and site (Mt. John and Port Levy). Photo taken September 1997. From left to right Port Levy centre, Mt. John centre, Port Levy outside, Mt. John outside.

Table 4.4 t-values and R² values from backwards step-wise multiple regression of *Hieracium pilosella* inflorescence initiation and daughter production vs. soil nutrients, pH or soluble aluminium. n.f. = not fitted (did not meet the criteria for inclusion in the model), * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$, ns = not significant (met the criteria for inclusion in the model but the effect was not statistically significant).

	Inflorescence initiation per rosette	Daughters per reproductive rosette
Site (MJ)	-4.10 **	n.f.
Position (o)	-2.66 *	n.f.
pH	3.33 **	n.f.
Ca	n.f.	n.f.
K	-4.31 **	n.f.
P	4.49 *	n.f.
Mg	n.f.	n.f.
Na	-4.83 ***	3.15 **
S	3.17 *	n.f.
Total N	n.f.	n.f.
Al	n.f.	-2.05 ns
R ²	0.882 ***	0.577 **

The proportion of rosettes initiating inflorescences was positively related to sulphur, phosphorus and pH of the soil but the number of daughters was not. There was a negative relationship between inflorescence initiation and potassium or sodium but potassium had no association with daughter production while sodium had a positive relationship. Calcium, magnesium and total nitrogen did not relate to reproductive success. Soluble aluminium had no association with the proportion of rosettes initiating inflorescences but had a (non-significant) negative relationship with the number of daughters produced (Table 4.4).

4.3.3 Growth rates

Growth ratios were similar for both sites. Longest leaf length ratio varied little between sites or patch position while rosette diameter ratios were slightly larger for soil from Port Levy and from patch centre soil at both sites. Wet weight ratios were greater at Port Levy than Mt. John and were greater for patch centres than outside patches for both sites (Table 4.5).

Table 4.5 Means \pm standard deviation, with sample number in parentheses for weight ratios of *Hieracium pilosella* plants grown in soil cores from within and outside Mt. John and Port Levy *H. pilosella* patches.

Site and position	Final to initial wet weight ratio	Final to initial longest leaf length ratio	Final to initial rosette diameter ratio	Final wet to final dry weight ratio
Mt. John centre	7.56 \pm 5.79 (22)	1.19 \pm 0.55 (24)	1.64 \pm 0.62 (24)	7.27 \pm 0.98 (22)
Mt. John outside	5.36 \pm 2.52 (19)	1.06 \pm 0.34 (22)	1.50 \pm 0.59 (22)	6.97 \pm 1.15 (19)
Port Levy centre	9.11 \pm 6.28 (19)	1.11 \pm 0.25 (22)	1.96 \pm 0.69 (22)	7.23 \pm 0.90 (19)
Port Levy outside	7.19 \pm 3.51 (11)	1.16 \pm 0.28 (20)	1.62 \pm 0.37 (20)	6.58 \pm 0.61 (19)

The wet:dry weight ratios for both sites were similar with the ratio being higher for patch centres than for outside patches. This suggests that plants grown in soil from the central region of a *H. pilosella* patch have higher water content than those grown in soil from outside a patch.

Table 4.6 General Linear Model results for final:initial weight ratios of *Hieracium pilosella* rosettes grown in soil cores from within and outside Mt. John and Port Levy *H. pilosella* patches. The growth ratios were log transformed before analysis. ** $p < 0.01$, * $p < 0.05$, ns = not significant.

(a) Final:initial rosette wet weight ratio.

	d.f	s.s	F ratio
Site	1	0.1196	5.63 *
Mainplot error	23	0.4851	
Position	1	0.0192	0.64 ns
Site \times Position	1	0.0048	0.16 ns
Subplot error	17	0.5079	
Total	43	1.1366	

(b) Final:initial longest leaf length ratio.

	d.f	s.s	F ratio
Site	1	0.0218	2.76 ns
Mainplot error	24	0.1895	
Position	1	0.0027	0.019 ns
Site \times Position	1	0.0013	0.09 ns
Subplot error	22	0.3155	
Total	49	0.5309	

(c) Final:initial rosette diameter ratio.

	d.f	s.s	F ratio
Site	1	0.0998	8.17 **
Mainplot error	24	0.2941	
Position	1	0.0370	2.6 ns
Site \times Position	1	0.0060	0.42 ns
Subplot error	22	0.3126	
Total	49	0.7494	

Table 4.6 Continued

(d) Wet:dry weight ratio.

	d.f	s.s	F ratio
Site	1	0.0009	0.36 ns
Mainplot error	23	0.0538	
Position	1	0.0047	1.33 ns
Site × Position	1	0.0000	0.00 ns
Subplot error	17	0.0601	
Total	43	0.1194	

The only significant effect on changes in growth of *H. pilosella* occurred between sites. Site affected both the change in diameter and the change in wet weight but had no effect on longest leaf length or the wet:dry weight ratio. Position and site × position did not affect any of the growth variates (Table 4.6a - d).

The final dry weights of plants grown in the soil from Port Levy were greater than those of plants grown in Mt. John soil, and plants from soil outside patches at Port Levy were heavier than those from within patches (0.97 g compared with 0.70 g; Table 4.7). There was little difference in dry weight at Mt. John for rosettes grown in soil from outside patches compared with those grown in soil from within patches.

Root weights for Mt. John soil were lower than for Port Levy, and lower from soil within patches than for soil outside patches at both sites. Shoot weights were greater for soil from outside patches at Port Levy than for all other soils. There was also a difference in the average root:shoot ratios between sites, with the ratios at Mt. John being lower than those at Port Levy (Table 4.7).

Total dry weight and root and shoot dry weight were mostly affected by the differences in site (Table 4.8a - c). Because the difference in dry weights from the two patch positions seemed especially prominent at the Port Levy site, further GLMs were conducted on the two sites separately. These analyses revealed no significant position difference in dry weights at Mt. John, but did show a significant position difference in total dry weight and shoot dry weight at Port Levy ($p = 0.016$ and 0.005 respectively).

Table 4.7 Mean dry weights \pm standard deviation for *Hieracium pilosella* plants grown in soil cores from within and outside Mt. John and Port Levy *H. pilosella* patches. Means are derived from plant dry weights recorded at the end of the glasshouse experiment.

Site/Position	n	Mean Dry Weight			
		Total (g)	Root (g)	Shoot (g)	Root:Shoot ratio
Mt. John centre	22	0.54 \pm 0.23	0.19 \pm 0.08	0.34 \pm 0.17	0.63 \pm 0.09
Mt. John outside	19	0.53 \pm 0.14	0.22 \pm 0.07	0.31 \pm 0.09	0.71 \pm 0.24
Port Levy centre	19	0.70 \pm 0.21	0.37 \pm 0.18	0.33 \pm 0.07	1.12 \pm 0.59
Port Levy outside	11	0.97 \pm 0.31	0.50 \pm 0.22	0.46 \pm 0.11	1.08 \pm 0.37

Table 4.8 General Linear Model for dry weight (g) of *Hieracium pilosella* grown in soil cores from within and outside Mt. John and Port Levy *H. pilosella* patches. Weights were log transformed before analysis. *** $p < 0.001$, * $p < 0.05$, ns = not significant.

(a) Total plant dry weight.

	d.f	s.s	F ratio
Site	1	0.4287	14.57 ***
Mainplot error	23	0.6767	
Position	1	0.0568	1.95 ns
Site \times Position	1	0.0029	0.10 ns
Subplot error	17	0.4953	
Total	43	1.6605	

(b) Total root dry weight.

	d.f	s.s	F ratio
Site	1	0.9947	22.62 ***
Mainplot error	23	0.0100	
Position	1	0.0876	2.85 ns
Site \times Position	1	0.0022	0.07 ns
Subplot error	17	0.5227	
Total	43	2.6172	

Table 4.8 continued

(c) Total shoot dry weight.

	d.f	s.s	F ratio
Site	1	0.1380	5.18 *
Mainplot error	23	0.6098	
Position	1	0.0473	1.48 ns
Site × Position	1	0.0175	0.54 ns
Subplot error	17	0.5449	
Total	43	1.3574	

While there is some difference in root:shoot ratio between patch position, the differences are not statistically significant. The only factor to affect this ratio was site related (Table 4.9).

Table 4.9 General Linear Model results for root:shoot ratio of *Hieracium pilosella* rosettes grown in soil cores from within and outside Mt. John and Port Levy *H. pilosella* patches. The growth ratios were log transformed before analysis. *** $p < 0.001$, ns = not significant.

LogRSR	d.f	s.s	F ratio
Site	1	0.3918	16.60 ***
Mainplot error	23	0.5422	
Position	1	0.0062	0.48 ns
Site × Position	1	0.0321	2.50 ns
Subplot error	17	0.2180	
Total	43	1.1902	

To show the relationship between total dry and wet weight a regression line was fitted to the average of pairs (Figure 4.3):

$$[\text{Dry weight}] = 0.1442[\text{Wet weight}]$$

$$t = 56.83, p < 0.001, R^2 = 0.8963$$

Results from the backwards stepwise regression are shown in Table 4.10. Sulphur had the greatest effect on the various weight ratios with calcium and sodium having the next

greatest effects. Phosphorus, magnesium and soluble aluminium had no effect on the different weight ratios.

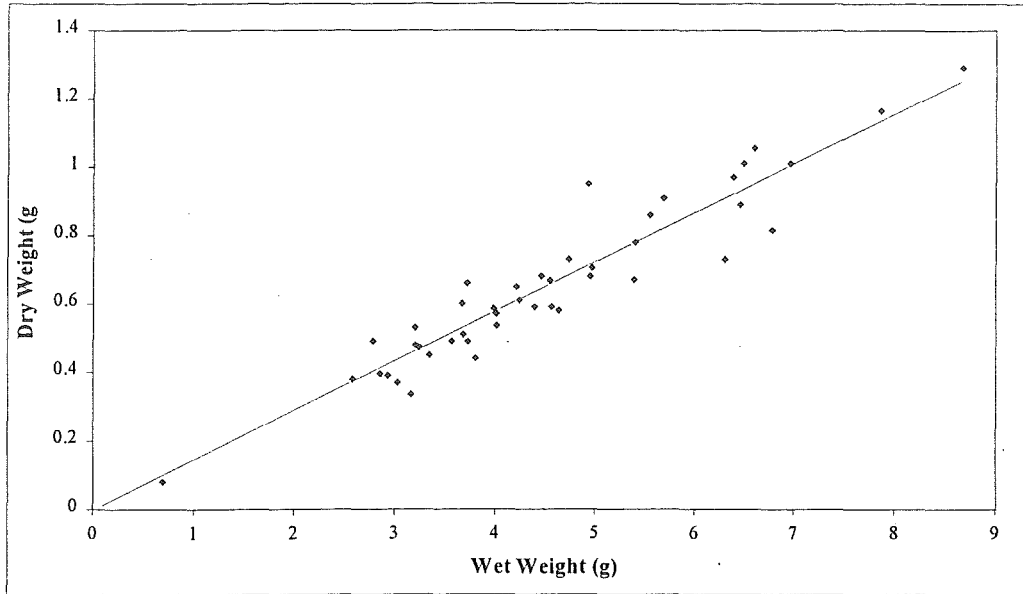


Figure 4.3 Regression fitted to mean final wet and dry weight for each central and outside patch pair.

Table 4.10 t-values and R^2 values from backwards step-wise multiple regression of *Hieracium pilosella* weight ratios and soil nutrient content. n.f. = not fitted, * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$.

	Final:initial longest leaf length ratio	Final:initial diameter ratio	Final:initial weight ratio	Root:shoot ratio
Site (MJ)	2.89 *	n.f.	n.f.	-3.12 *
Position (o)	4.06 **	n.f.	n.f.	-2.89 *
pH	-4.25 **	n.f.	n.f.	2.67 *
Ca	7.28 ***	3.71 **	4.40 ***	n.f.
K	2.69 *	n.f.	n.f.	n.f.
P	n.f.	n.f.	n.f.	n.f.
Mg	n.f.	n.f.	n.f.	n.f.
Na	3.22 **	n.f.	-2.32 *	-4.63 ***
S	4.30 ***	4.35 ***	3.71 **	3.01 *
Total N	n.f.	n.f.	n.f.	-3.50 **
Al	n.f.	n.f.	n.f.	n.f.
R^2	0.791 ***	0.547 **	0.586 **	0.815 ***

4.4 Discussion

With the effects of immediate competition for space, light and water removed and the source plants taken from a single location, this experiment provides a useful insight into why areas with a long history of *Hieracium pilosella* occupation begin to show increasing amounts of bare ground. Plants grown in soil from areas at Port Levy in which there was no previous history of *H. pilosella* had a higher proportion of reproductive rosettes, produced more daughter rosettes and produced more stolons of longer length (Table 4.11). In addition, the experiment suggests that the longer the history of *H. pilosella* presence, the more that reproduction and growth rates are adversely affected. The relative equality in reproductive output from plants grown in soil cores from Mt. John was to be expected because areas without *H. pilosella* were small and cores from outside *H. pilosella* patches generally came from areas of less than 0.5 m in diameter. Being so close to *H. pilosella*, it would be unlikely that the area was not affected in some way by the surrounding plants. In addition, due to the long occupation of *H. pilosella* at Mt. John, it is likely that these “outside” areas have supported *H. pilosella* in the past. Effectively this means that only one of the treatments, Port Levy outside, had no history of *H. pilosella* occupation.

With the exception of calcium and phosphorus, all other soil nutrients, soil acidity and soluble aluminium were significantly lower in the Mt. John soils than the Port Levy ones (Table 4.11). At Port Levy, there were higher concentrations of sodium and sulphur in patch centres and at Mt. John, phosphorus was higher in patch centres. As found in other studies (Scott 1975; McIntosh & Allen 1993; McIntosh *et al.* 1995; Espie & Boswell unpublished manuscript), pH was lower in patch centres than outside patches at Mt. John, but contrary to these, there was no difference in pH between soil cores from outside patches and patch centres at Port Levy.

There are several possible explanations for the differences in reproductive vigour and growth rates between sites or patch position at Port Levy. One may be the suspected allelopathic abilities of *H. pilosella*. Allelopathy, the inhibition of one plant by the production of chemicals by another plant of the same or different species, has been suggested as a reason for the success of *H. pilosella* in some areas of New Zealand and may also explain the bare areas within patches (Guyot cited in Widera 1978). Widera

(1978) found that extracts from the root zone and from fresh plants of *H. pilosella* inhibited the germination of seedlings and growing fragments of both *H. pilosella* and *Festuca rubra*. She concluded that allelopathic activity was the mechanism by which *H. pilosella* out competed *F. rubra* in the field.

Table 4.11 Summary of results for various differences between soil cores taken from *Hieracium pilosella* patch centres and areas outside of patches at Mt. John and Port Levy. "+" signifies an increase in the variate, "-" signifies a decrease in the variate. 0 = no difference, +/- $p < 0.05$, +/- $p < 0.01$ and +/- $p < 0.001$.

Variable	Site difference	Patch centres vs. outside	
	Mt. John vs. Port Levy	Port Levy	Mt. John
pH	+++	0	--
Al	---	0	+
Ca	+++	0	0
K	---	0	0
P	0	0	+++
Mg	---	0	0
Na	---	+	0
S	---	+	0
TN	---	0	0
Rosette reproduction	0	---	0
Daughter production	-	---	0
Root:shoot ratio	---	0	0
Wet weight ratio	-	0	0
Diameter ratio	--	0	0
Longest leaf length ratio	0	0	0

Makepeace *et al.* (1985) identified umbelliferone as the most active phenol in *H. pilosella* and found it to occur only in the leaves. In laboratory trials they demonstrated that extracts from dead *H. pilosella* leaves reduced the rate of germination in *Trifolium repens* and caused abnormalities in the root growth of seedlings of 8 species including *H. pilosella* itself. They also found that growth was inhibited in *Dactylis glomerata* and *T. repens* when recently dead *H. pilosella* leaves were placed on the surface of the soil in a pot experiment.

In contrast, evidence of allelochemicals has not been detected in soils sampled from under *H. pilosella* (Makepeace *et al.* 1985; Henn *et al.* 1988). However, Makepeace *et al.* (1985) suggested that the effect would be ephemeral in the field, with significant levels only occurring under certain conditions such as after a drought which killed leaves and was then followed by rain. In addition, Henn *et al.* (1988) found no evidence of allelopathic effects of *H. pilosella* on the germination or growth of *Arrhenatherum elatius* in a glasshouse experiment. They concluded that there was no accumulation of phenols in the soil and suggested that *H. pilosella* did not conform to the definition of an allelopathic species.

Allelopathy seems unlikely as an explanation for the differences encountered between Mt. John and Port Levy, and between patch positions at Port Levy. Since umbelliferone has not been shown to accumulate in the soil, the likelihood of the plants grown in Mt. John or Port Levy soil from patch centres encountering higher amounts of the chemical is small. All plants received the same amount of water so that any leaching from dead leaves would have been equivalent between treatments. If anything, those plants grown in Port Levy soils may have been subjected to higher amounts of umbelliferone. If leaf turnover rates are assumed to be the same, the higher growth rates and larger sizes of Port Levy rosettes may have resulted in the biomass of dead leaves being greater, resulting in an increase of source material for allelopathic chemicals. Although the lower root biomass at Mt. John would be consistent with a soil-borne auto-allelopathic effect, many other physical soil variables can alter root growth. Therefore, this study provides no direct support for the existence of an allelopathic effect *per se* in *H. pilosella*.

Another possible cause for the reduced vigour in the plants grown in soil for Mt. John may be an increase in soluble aluminium in soils under patches of *H. pilosella* plants. Espie and Boswell (unpublished manuscript) examined soils from under *H. pilosella* plants and surrounding grasses and found that soluble aluminium was greater under the patches than in either surrounding vegetation or central bare regions of patches. They attributed this increase in soluble aluminium to the decrease in pH which has been shown to occur in soils under *H. pilosella* (Scott 1975; McIntosh & Allen 1993; McIntosh *et al.* 1995; Espie & Boswell unpublished manuscript). This increase in soluble aluminium would also have toxic effects on other resident plant species.

In this study, the trend of lower pH under *H. pilosella* than non-*H. pilosella* areas was supported by soil samples at Mt. John and the decrease in pH coincided with an increase in soluble aluminium. When reproductive attributes were regressed against different soil components, the number of daughters per reproductive rosette decreased non-significantly under higher soluble aluminium levels while the number of reproductive rosettes was not affected. While the decrease was insignificant, the effect of soluble aluminium was significant enough to be included in the model. This suggests that while the proportion of rosettes reproducing may remain constant under varying levels of aluminium, the number of daughters they produce might differ; as aluminium levels increase, rosettes reproduce (and die) but recruitment decreases. If recruitment levels fell below mortality levels, a decrease in the number of rosettes would occur, which might be a partial explanation for the thinning often seen in patch centres. However, pH and soluble aluminium levels at Port Levy were not significantly different. This suggests that, at least at Port Levy, the aluminium hypothesis does not apply. Some other factor must account for the marked effects of position at Port Levy.

Because the glasshouse experiment removed the effects of competition for light, water and space and differences in reproductive vigour and growth cannot be solely attributed to allelopathy or aluminium toxicity, nutrient differences may be the cause of the variation in growth and reproduction between the two sites and between patch position at Port Levy. Several studies have looked at changes in reproductive rates with respect to soil nutrients (Davy & Bishop 1984; Svavarsdóttir 1995; Fan & Harris 1996). In all cases, *H. pilosella* showed an increase in reproductive activity with increased fertility. In a field experiment in Breckland, Davy and Bishop (1984) described an increase in stolon and inflorescence production with the addition of nutrients, nitrogen being particularly important. Svavarsdóttir (1995) found that stolon production and flowering of *H. pilosella* grown in the glasshouse occurred only in plants which received additional phosphate although the addition of nitrogen was preferable as well. Makepeace (1985b) showed that *H. pilosella* increased stolon number and length with the addition of nitrogen and superphosphate respectively. Although the effect of individual nutrients was not tested, Fan and Harris (1996) saw an increase in flower stalks when overall fertility was increased.

Nutrients have also been shown to cause a difference in yield of *H. pilosella* in pot or glasshouse experiments. In a glasshouse experiment Svavarsdóttir (1995) showed that the diameter of *H. pilosella* plants increased as did total biomass when nitrogen, phosphate and/or micronutrients were added to the pots. When above- and below-ground biomass was analysed separately, she found that phosphate stimulated shoot and root growth. Similar results were described in a glasshouse experiment by Makepeace (1985b) and in a garden experiment by Fan and Harris (1996). Nitrogen, in contrast, depressed above ground growth of *H. pilosella* in the absence of phosphate and depressed below ground growth regardless of whether phosphate was added or not (Svavarsdóttir 1995). This contrasts with results obtained by Makepeace (1985b) in his glasshouse trial in which nitrogen stimulated growth even in the absence of phosphate.

In contrast to the glasshouse and garden experiments mentioned above, field experiments have shown a decrease in abundance of *H. pilosella* when additional nutrients were added (Davy & Bishop 1984; Scott & Covacevich 1987; Scott 1993a). In all these studies, vigorous growth of other species occurred in conjunction with the decline of *H. pilosella*. Davy and Bishop (1984) suggested that the decline in *H. pilosella* under higher nutrients was due to the increase in inflorescence initiation, hence an increase in mortality, of *H. pilosella* coupled with an increase in the competitive advantage of resident grasses.

4.5 Conclusions

In this study, the most dramatic increase in inflorescence, stolon, and daughter production was in cores which came from the outside of *Hieracium pilosella* patches at Port Levy, the only site likely never to have supported *H. pilosella* in the past. In light of past studies, it would be expected that these soils would be higher in nutrients than the other soils. However, while soils at Port Levy had higher levels of most nutrients than Mt. John, there was little difference between the nutrient content of soils from outside patches and patch centres. The main difference between the two positions was a greater amount of sulphur and sodium in central patch soils.

If success of a plant is determined by reproductive vigour, results from this experiment suggest that *H. pilosella* is more vigorous in soil in which it has not previously grown.

Such soils had a greater proportion of reproductive rosettes and a greater number of daughters produced than soils which had a history of *H. pilosella*.

The study provides no direct support for the existence of an allelopathic effect *per se* in *H. pilosella*, nor does it provide evidence of aluminium toxicity. While there were differences in pH at Mt. John between patch 'centres' and 'outside' patches, there was no way to be certain that *H. pilosella* was not affecting the 'outside' soils due to the overall degraded nature of the Mt. John site and its long history of *H. pilosella* occupation. In addition, at Port Levy, where patches could easily be discerned from surrounding vegetation, there was no difference in pH levels between patch centres and outside patches.

The differences recorded in glasshouse rosettes are more likely to be related to nutrient differences, with sodium and sulphur possibly having the greatest effect on growth rates and inflorescence initiation. The effect of nutrient levels is clearly more complex in the field since the outcome also depends on competition and *H. pilosella* is less competitive in nutrient-enriched soils.

5. Modelling Population Dynamics and Biological Control of *Hieracium pilosella*

5.1 Introduction

The economic cost of land infested with *Hieracium* spp. has been estimated to be in the millions of dollars annually (Grundy 1989) and methods currently available to control these weeds are either too expensive or impractical. Widespread use of fertiliser and oversowing is one approach to controlling *Hieracium pilosella* (Cossens & Brash 1980; Scott 1985 & 1993a; Scott *et al.* 1990a) but this is only suitable on better soils (Scott 1985; Scott *et al.* 1990a). As an alternative, high country areas could be converted for use in agro-forestry (Espie 1994), however there are land use planning and landscape amenity issues to be resolved before this could become widespread. Biological control by one or more agents offer one of the few feasible options for reducing the density of a widespread weed such as *H. pilosella*.

To date, there have been 4 insect species and a rust identified as potential control agents for *H. pilosella* (Syrett & Sárospataki 1993; Jenkins 1995; Syrett *et al.* 1996). The rust, *Puccinia hieracii* var. *piloselloidarum*, has been released at several sites in the South Island and its spread is being monitored (T. Jenkins and D. Scott, *pers. comm.*). Two of the insects, *Oxyptilus pilosellae* (Lepidoptera: Pterophoridae) and *Aulacidea subterminalis* (Hymenoptera: Cynipidae), have been brought into New Zealand under quarantine and must undergo further species specificity tests before they can be considered for release. The other two insect species, *Macrolabis pilosellae* (Diptera: Cecidomyiidae) and *Cheilosia praecox* (Diptera: Syrphidae), are expected to be brought into quarantine in the near future (P. Syrett, *pers. comm.*).

Understanding the dynamics of a pest population is a pre-requisite for effective biological control. The use of models in selecting and releasing potential control agents will not remove the uncertainty of whether the introduction will be successful but they do help in making more educated decisions and can reveal possible problems or outcomes which may have been overlooked (see for example Barlow & Goldson 1990 & 1993; Hoffmann 1990; DeGrandi-Hoffman *et al.* 1994; Barlow in press).

The purpose of this study is to develop models to describe the basic population biology of *H. pilosella* and use these models to predict the potential impact of different types of

biological control agents, not only on population density but also on the area covered by the weed. Once more is known about the population ecology of specific control agents in New Zealand and their effect on *H. pilosella*, it will be possible to incorporate their population dynamics into the models. This will help in monitoring the effectiveness of the agents after release and providing early prognoses for their ultimate impact. If unsatisfactory, additional species can be considered for release.

The first part of this chapter explores two spatial cellular automata models based on *H. pilosella* data extracted from Makepeace's study (1980) and data from the Mt. John population presented in Chapter 2. The cellular automata models were chosen because they provide a way of determining a population's spread over time based on simple rules, and they provide a visual mechanism for exploring patterns of spread. The second part of the chapter compares three additional models based on the Mt. John data only. The first is a coupled map lattice model used to predict the spread of *H. pilosella* over a larger area. The second is a non-spatial Ricker model and the third a spatial analytical model. The coupled map lattice and Ricker models are used to determine the effect of additional fertiliser and water on *H. pilosella* populations as well as the effect of different types of biological control, allowing for a comparison between two modelling techniques. The spatial analytical model describes the spatial spread of populations through time.

5.2 Methods

5.2.1 Spatial cellular automata models

Cellular automata (CA) models are discrete models in which space is depicted as an array of interacting cells. Cells are usually represented by a 2-dimensional grid in a rectangular arrangement with each cell representing the state of a variable in the system being modelled. In population dynamic models these cells may represent small areas which an organism can occupy. At each time step, the cell's state is updated according to transition rules which depend on the cell's current state and the state of its defined neighbour cells. For example, a cell may contain a plant which has a chance of dying or reproducing, or it may be an empty cell able to be colonised by a plant from an adjacent cell.

Cellular automata models have been used in a variety of natural systems. These include the growth of dendritic crystals (e.g. snowflakes), turbulent fluid movement, biological pattern formation such as pigmentation patterns on mollusc shells (Wolfram 1984) or clonal plant growth patterns (Cain & Cook 1988; Cain 1990; Callaghan *et al.* 1990; Cain, Pacala & Silander 1991 & 1995), and host-parasitoid systems (Hassell *et al.* 1991; Comins, Hassell & May 1992). In the past, cellular automata models of clonal plants were primarily morphological (i.e. architectural) models rather than population models and were concerned with the spatial arrangement of ramets (e.g. angle between nodes) or the rate of clonal expansion into new habitat based on the observed patterns of clonal growth (Cain & Cook 1988; Cain 1990; Cain *et al.* 1991). More recently, however, there has been a shift to more demography-based models which incorporate spatial and local interactions, births and deaths of plants and the morphological details of clonal growth (Callaghan *et al.* 1990; Cain *et al.* 1995).

The models described here predict the spatial spread of a *Hieracium pilosella* patch, using variations in vital rates within different zones of a patch as described by Makepeace (1980) and the spread of mature populations using data from the Mt. John population described in Chapter 2. While the two models are similar in their construction and output, it is difficult to compare their predictions for spread other than at a very basic level, because the data sets used in their formulation are inherently different. For example, at Wolds, Makepeace was able to differentiate between high-*Hieracium* and low-*Hieracium* zones within a patch and describe the differences in daughter production between these zones, whereas the Mt. John data are based on the overall dynamics of the population because discernible patches did not exist. In addition, Makepeace suggested that mortality was restricted to reproductive rosettes, whereas at Mt. John mortality was density-dependent and consisted of reproductive and non-reproductive mortality.

5.2.1.1 Starting conditions

In both cellular automata models, space is represented by a 50 x 50 square lattice depicting a homogeneous patch of ground. Lattice size was chosen to determine patch spread in the absence of boundary conditions, although the size can be expanded or reduced as required.

To estimate the change in population density through time, 50 rosettes were initially distributed randomly over the grid. This was to simulate the initial establishment of rosettes from seed into a previously *H. pilosella*-free space. Once the change in rosette density through time was simulated, the model results were also expressed in terms of cover using regression equations derived in Chapter 2. To estimate patch spread, a single rosette was placed in the central cell. In both cases, the grid was free from other species and thus represents *H. pilosella* population changes in a uniformly favourable environment.

5.2.1.2 Cell states

An individual rosette was allowed to occupy only one lattice cell and each cell could be assigned to one of five states depending on the time step and model: rosette, daughter, marsupial, zombie or empty. The five states are defined as follows:

Rosette - A single adult rosette;

Daughter - A new single daughter rosette produced during the spring/summer time step;

Marsupial rosette - A rosette which has produced an axillary daughter and will be replaced by this daughter in the next time step. This state only occurs in the Wolds CA model because of the difficulty in differentiating between rosette and daughter mortality during the course of the Mt. John field study;

Zombie rosette - A rosette which will die due to flower production, or from some external cause during the autumn/winter time step but is currently occupying the cell during the summer period. As with the marsupial rosette, this state only occurs in the Wolds CA model;

Empty - Bare ground.

The only overlap allowed between individual rosettes within a cell was during the spring/summer time step where an axillary daughter rosette could replace its parent who had not yet died. Germination and survival of seedlings in populations of *H. pilosella* was rare (Makepeace 1980; Chapter 2, this thesis), thus seedling recruitment was not

addressed in this model. Each year was divided into two time steps: spring/summer (flower and daughter production) and autumn/winter (mortality). The neighbourhood of a cell was defined to be a Moore neighbourhood (Czárán 1998) in which neighbours are composed of one or more concentric zones (the neighbourhood radius) around a central cell (Figure 5.1).

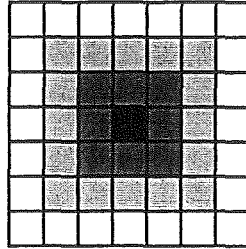


Figure 5.1 The neighbourhoods (shaded) around a focal cell (black). A radius of 1 (dark grey) includes the surrounding 8 cells, a radius of 2 (light grey) includes the surrounding 24 cells and a radius of 3 (white) includes the surrounding 48 cells of the focal cell.

5.2.1.3 *Daughter production and dispersal*

Transition between states within a cell was dependent on the number of non-empty cells within a defined neighbourhood of the occupied cell. In the Wolds CA model, if a cell was in the interior of a patch (defined as having more than 70% of the neighbouring cells occupied within a radius of 3), the probability of inflorescence initiation was less, the number of daughters produced was fewer and the distribution radius (the number of concentric zones available for distribution) was smaller than for a cell on the edge of a patch. This was to simulate Makepeace's finding that interior rosettes had a lower probability of initiating an inflorescence, gave rise to fewer daughters per rosette and formed stolons of shorter length than edge rosettes (Makepeace 1980). The number of daughters produced was found to follow a Poisson distribution, hence the number of daughters was determined by a Poisson random number with mean μ . μ is the expected number of daughters per rosette determined by the rosette's patch position.

The following transition rules were used in the Wolds CA model:

Summer time step:

For each cell containing a rosette, the number of daughters produced was randomly selected from a Poisson distribution based on its patch position. If the number of daughters produced was more than 0 then the cell either became a zombie or marsupial rosette depending on a uniform random number selected between 0 and 1 and its patch position: edge rosettes had 0.80 probability of producing an axillary rosette and central rosettes had a 0.95 probability (Makepeace 1980);

An empty cell became a daughter if it was within the dispersal radius of a daughter producing rosette and if a random number between 0 and 1 was less than

$$\frac{\text{Number of daughters not yet allocated a cell}}{\text{Number of remaining empty cells}} \text{ in the dispersal neighbourhood.}$$

Winter time step:

Zombie rosettes died and the cell became empty;

Daughters and marsupial rosettes became rosettes.

Parameters used in both models are shown in Table 5.1. The parameters for the Wolds CA model came from Makepeace's data for patch interiors and edges at Wolds, South Island, New Zealand (1980). Reproductive rates were calculated by using a Poisson distribution to determine daughters per rosette given the probability of a rosette not initiating an inflorescence. It is important to note that in this model there was no mortality due to non-reproductive events. While non-reproductive mortality is likely to occur in *H. pilosella*, Makepeace gave no data and stated that "mortality was entirely restricted to reproductive plants" during the duration of his study (Makepeace 1980), hence, mortality rates were based solely on the probability of reproducing. The daughter dispersal radius was based on the total stolon length for patch interiors and edges.

Table 5.1 Reproductive, survival and dispersal parameters used in the cellular automata models. The Wolds CA model parameters are based on a study by Makepeace (1980) and the Mt. John CA model parameters are based on the 1994 - 1996 Mt. John data (Chapter 2) from those plots which did not receive additional water, nutrients or cutting. In the regression equation R = number of rosettes and D = number of daughters in the neighbourhood. Neighbourhood radius was used to determine density while dispersal radius determined the cells available for daughter dispersal.

Model-patch position	Daughters per rosette	Mortality	Neighbourhood radius	Daughter dispersal radius
Wolds-edge	0.476	0.379	3	3
Wolds-interior	0.018	0.018	3	1
Mt. John-all	0.202	$0.00593 * (R + D) + 0.0085$	3	2

The long-term presence of *H. pilosella* at Mt. John has resulted in the amalgamation of individual patches to the extent that the whole trial site can be considered a patch interior. It was therefore necessary to alter the Mt. John CA model to account for this difference. As in the Wolds CA model, daughter production was determined by a Poisson random number with mean μ equal to the expected number of daughters per rosette. However, the number of daughters produced and the dispersal radius was the same for all cells; it did not vary with patch position nor did it vary with density (Chapter 2). Mortality, on the other hand, was found to be density-dependent at Mt. John (Chapter 2) so the mortality rate was calculated for both daughters and rosettes based on a regression equation derived from the two years of data for untreated plots described in Chapter 2 ($n = 60$, $F = 18.17$, $p < 0.001$). From the field study the maximum density (rosettes and daughters) in any 49 cm² quadrat was approximately 50 rosettes so for simplicity, mortality was based on the number of non-empty cells in a focal cell's neighbourhood (i.e. 48 surrounding cells plus the focal cell).

The transition rules used in the Mt. John CA model were as follows:

Spring/Summer:

Daughter production for each rosette filled cell was determined using a random number from a Poisson distribution;

An empty cell became a daughter if it was within the dispersal radius of a reproducing rosette and if a random number between 0 and 1 was less than
$$\frac{\text{Number of daughters not yet allocated a cell}}{\text{Number of remaining empty cells}}$$
 in the dispersal neighbourhood.

Autumn/Winter:

Mortality of rosettes and daughters was randomly determined based on neighbourhood density and the regression equation. If a random number was less than the derived mortality rate, the cell became empty;

Surviving daughters became rosettes.

The parameters for the Mt. John CA model (Table 5.1) came from data collected in this study. They were based only on those plots which did not receive extra water, nutrients or cutting. Marsupial and zombie rosettes were not incorporated into this model because of the difficulty in differentiating between rosette and daughter mortality during the course of the field study; the mortality equation is based on the total population of rosettes and daughters irrespective of whether they had reproduced.

5.2.1.4 *Boundary conditions*

Treatment of cells at the grid boundary can be dealt with in three ways (Comins *et al.* 1992). The first is an absorbing boundary in which individuals of the population are lost when they disperse across the boundary. The second is a reflective boundary in which individuals at the boundary edge remain at the edge and are not lost. The final boundary type is a cyclic boundary in which opposite edges of the boundary are joined together to form a torus. It was decided to use a cyclic boundary in these models to avoid edge effects. The use of this type of boundary condition is reasonable so long as the lattice is large compared with individual rosettes (van Tongeren & Prentice 1986). Further boundary effects were avoided by only presenting results from the central 47×47 cells when determining patch spread, thus leaving a 3 cell buffer zone around the grid edge.

5.2.2 Spatial coupled map lattice model

The coupled map lattice model, in which each cell depicts a population rather than a single individual, is a spatial expansion of true cellular automata models. It extends the area covered by the model as well as allowing for varying micro-habitats in which reproductive and mortality rates differ due to soil nutrients, competitor species, grazers etc. In a coupled map lattice model, the dynamics within a cell are assumed independent of other cells on the grid; all reproductive and mortality rates are based solely on the population within the particular cell.

Coupled map lattice models were first developed by Kaneko (1989) to examine spatiotemporal chaos. The technique was then adopted to model host-parasitoid systems (Hassell *et al.* 1991; Comins *et al.* 1992), parasitoid coexistence (Hassell, Comins & May 1994; Comins & Hassell 1996) and neighbourhood competition effects or herbivory effects on single species plant populations (Hendry, McGlade & Weiner 1996; Rees & Paynter 1997).

This coupled map lattice model was developed to analyse the spread of *H. pilosella* over a larger area and to simulate the population dynamics under different environmental conditions or in the presence of biological control agents. With the type of data available, this approach could only be applied to the Mt. John site. The model was selected because it alleviated the need for “marsupials” and “zombies” and it allowed more versatility for future modelling applications (e.g. adding in population dynamics of biological control agents).

5.2.2.1 Starting conditions

As in the cellular automata models, a 50×50 lattice was used with each cell now representing an area rather than the state of a single rosette. The area represented by each cell in this model is equal to the size of the subplots used in the Mt. John study (i.e. 7×7 cm).

Non-empty cells can contain 1 to many, although usually not more than 50, rosettes. The density within a cell depended on the production and dispersal of daughter rosettes from within the cell and from neighbouring cells.

As in the cellular automata models the time step was half a year with the two half years corresponding to autumn/winter and spring/summer. Neighbour cells consisted of the 8 surrounding cells. Because the population at Mt. John was assumed to be mature, the spread of the population in this model depicts the movement of *H. pilosella* in areas with a history of *H. pilosella* occupancy.

To determine the spread of *H. pilosella* through space and time, the central cell was seeded with an initial density of either 5 or 20 rosettes to determine whether initial cell density had an effect on spread. Spread was assessed in two ways, based on the spreading 'front' (i.e. using cells containing at least 1 rosette) and based on the spreading iso-concentration ring of cells at half the equilibrium density (i.e. using cells containing at least 11 rosettes). In both cases, the patch diameter at any time was taken to be the number of cells along a fixed axis through the initially-seeded cell, whose rosette density exceeded 1 or 11 respectively.

Model runs were repeated for the different boundary conditions to test whether there were any discrepancies in population size. Since there were no differences in steady states and spread was determined using the central 47×47 cells, the cyclic boundary condition was used.

To establish the effects of biological control or environmental manipulations, the model was initialised with each cell containing 21 rosettes, the steady-state density of the model under control conditions. The change in population densities was then determined for each manipulation by averaging the density of all cells through time until a steady state was reached.

5.2.2.2 *Reproduction, mortality and dispersal*

Daughter production and mortality rates for the control simulations were similar to those used in the Mt. John CA model (Table 5.1). In each cell, the number of daughters per rosette was determined as a Poisson random number with the mean equal to the product of the number of rosettes within the cell and the mean number of daughters per rosette. Mortality rates for both daughters and rosettes were derived from the density-dependent regression equation (Table 5.1) The number of deaths per cell was determined by a

Poisson random number with the mean equal to the product of the mortality rate and the number of daughters and rosettes in the cell.

Movement between cells by daughter rosettes was simulated as a stochastic event. It was found from the field data (Chapter 2) that approximately 8% of the daughters produced from within a quadrat established outside it. Hence, the number of daughters which would establish outside its parent cell was based on a Poisson random number with mean equal to 8% of the number of daughters produced. One of the 8 neighbour cells was randomly selected for each ‘emigrating’ daughter.

5.2.2.3 *Environmental and management effects*

The effects of environmental conditions or management practices were tested in the model by replacing the reproductive rate and mortality equation with those determined by the relevant treatment. Since only the fertiliser and water × fertiliser trials affected mortality and daughter production, these were the only treatments simulated. The parameters and equations used for their environmental effects are given in Table 5.2.

Table 5.2 Reproductive rates and mortality equations used in the coupled map lattice model to determine the effects of fertiliser or fertiliser + water on the density and cover of *Hieracium pilosella* at Mt. John. R = Rosette, D = Daughter. Values were derived from data collected in the Mt. John study (Chapter 2). See text for details on how regression equations were derived.

Treatment	Daughters per rosette	Mortality rate
Control	0.202	$0.0059*(R + D) + 0.009$
Fertiliser	0.344	$0.0059*(R + D) + 0.344$
Fertiliser + water	0.265	$0.0059*(R + D) + 0.129$

The daughter production rate for the control treatment was taken to be the annual mean number of daughters per rosette calculated from two years of data collected in the control plots, whereas the values for the fertilised and fertilised + watered were derived from data collected in the first year from the corresponding plots. Because two years of data were available for the control plots and only one year for the treatment plots, the slopes of the regression lines for each treatment separately and for all data together were compared following the methods described by Snedecor and Cochran (1980). None of the slopes were significantly different so, for consistency, the mortality equation for the control was

the same as that used in the cellular automata models. The treatment equations were derived by using the same slope as the control equation and calculating the mean mortality rate and density from the one year of data in the corresponding plots and determining the intercept.

5.2.2.4 *Biological control*

When modelling the biological control of a species with density-dependence it is important to consider where in the life cycle the biological control occurs (Wang & Gutierrez 1980; May *et al.* 1981), particularly the order in which control mortality and density-dependent mortality act. If control mortality occurs before density-dependent mortality, it is also necessary to consider whether density-dependence acts on only that part of the population not affected by the control agent or on the total population. This is particularly important if the control agent does not kill its host immediately. In this situation the density-dependence not only affects the host population but may also affect that of the control agent. This is especially likely for parasitoids, when density-dependent mortality may occur in both parasitized and unparasitized hosts resulting in the death of a proportion of the parasitoid population. Thus, the parasitoid's mortality is dependent on the density of the host.

In the case of *H. pilosella*, the life cycles of the control agents are not yet fully understood. Consequently, and as has been the convention for weed biological control models (Barlow in press), biological control is simulated either as an additional mortality or an effect on reproductive rates in the form of reduced daughter production. In this model, additional mortality was applied either before or after the post-reproductive density-dependent mortality to determine if there is an optimal time for the biological control agent's action.

5.2.3 **Non-spatial Ricker model**

There have been several different single-species models published to describe population growth in both continuous and discrete time (see reviews by May & Oster 1976; Bellows 1981). When determining the form of a population growth function, it is important to choose one that is both realistic and simple. *H. pilosella* could conceivably be modelled either in discrete or continuous time since reproduction occurs during a particular time of

year but generations overlap. It was decided to use the discrete Ricker model for its simplicity and its ability to describe a density-dependent population in the absence of specific density-dependent mechanisms. The model was used to simulate the change in density and cover of *H. pilosella* over time in the presence and absence of biological or other control.

The general form of the Ricker model is

$$N_{t+1} = N_t e^{r(1-N_t/K)}$$

where N_t is the population size at time t , r is the population's growth rate and K is the carrying capacity or equilibrium density.

To incorporate density-dependent mortality acting on both parent and progeny, the basic form of the Ricker model was modified as follows:

$$N_{t+1} = aN_t(1+R)e^{-bN_t(1+R)}$$

where N is rosette density at time t , a is the density-independent survival rate, b is the density-dependent mortality coefficient and $R = 0.202$ is the reproductive rate derived from the control plots (Chapter 2). Hence, mortality is acting on the total population of rosettes and daughters, $N_t(1+R)$. In this form of the equation, $a(1+R)$ is the maximum rate of increase and $[\ln(a(1+R))]/b(1+R)$ is the carrying capacity.

The values for a and b were derived by fitting the modified Ricker equation to data from Mt. John by the non-linear fit command in Genstat 5 (Genstat 5 Committee 1993) ($r^2 = 0.921$) and are as follows: $a = 0.988$ and $b = 0.006$.

5.2.3.1 Biological control

As in the spatial model, the timing of mortality caused by a biological control agent is important. When the population dynamics of the control agent are known, there are three scenarios to consider (May *et al.* 1981). As a general case, suppose that a population of size N_t has a constant, density-independent finite rate of increase λ , and a density-dependent survival rate $s(N_t)$. Let $f(N_t, P_t)$ be the proportion of N_t which escapes

predation by P_t the population of predators. Then according to May *et al.* (1981) the three scenarios that can occur are as follows:

Biological control before density-dependence:

$$N_{t+1} = \lambda N_t f(N_t, P_t) s(N_t f(N_t, P_t)) \quad (1)$$

Density-dependence before biological control:

$$N_{t+1} = \lambda N_t f(N_t s(N_t), P_t) s(N_t) \quad (2)$$

Density-dependence acts on control agent as well as host population:

$$N_{t+1} = \lambda N_t f(N_t, P_t) s(N_t) \quad (3)$$

In the case of the *H. pilosella* model presented here, biological control is represented as an additional proportional mortality, say m . This results in f being a constant equal to $1 - m$, independent of the density of either N (rosettes) or P (biological control agent). Hence, equations (2) and (3) reduce to the same equation.

For the Ricker model used in this study adding the effects of biological control before and after density-dependence results in the following two models:

Mortality before density-dependence:

$$N_{t+1} = a(1 + R)(1 - m)N_t e^{-bN_t(1+R)(1-m)} \quad (4a)$$

Mortality after density-dependence:

$$N_{t+1} = a(1 + R)(1 - m)N_t e^{-bN_t(1+R)} \quad (4b)$$

where equation (4a) is equivalent to May *et al.* (1981) equation (1) and equation (4b) is equivalent to their equations (2) and (3).

A final case to consider is when the control agent affects only the reproductive ability of the pest. This form of control would be equivalent to a reduction in R by m . The resulting model is:

Biological control affecting reproduction:

$$N_{t+1} = a(1 + R(1 - m))N_t e^{-bN_t(1+R(1-m))} \quad (4c)$$

5.2.4 Analytical spatial model

An analytical model was developed to summarise and succinctly portray spatial as well as temporal dynamics of the Mt. John *H. pilosella* population. To this end, the rate of increase estimated from the Ricker model and daughter distance measured from the initial mapping of rosettes at Mt. John were used to parameterise a Fisher diffusion model for two-dimensional space with logistic growth (Fisher 1937). Predictions of rate of spread were then compared with those of the explicit spatial models.

The velocities of spread in the explicit spatial models were derived by determining the slope of the line relating patch diameter to time (in years). In the case of the spatial cellular automata model, it was assumed that each cell was equivalent to 1 cm² because field observations suggested an upper limit of approximately 50 plants per 49 cm² area. In the coupled map lattice model, each cell depicted a 49 cm² area.

Fisher's two-dimensional diffusion equation for logistic population growth is given by

$$\frac{\partial n}{\partial t} = D \left(\frac{\partial^2 n}{\partial x^2} + \frac{\partial^2 n}{\partial y^2} \right) + (\varepsilon - \mu n)n$$

where $n(x, y, t)$ denotes the population density at time t and the spatial coordinate (x, y) , D is the diffusion coefficient in two dimensions, ε is the intrinsic rate of increase and $\mu(\geq 0)$ is the effect of density-dependence on the rate of increase. From this diffusion equation, Fisher determined the rate of expansion to be $2\sqrt{\varepsilon D}$ (where ε and D are defined as above). This is equivalent to the rate of expansion derived by Skellam (1951) for diffusion in a population with exponential growth (Okubo 1980). Using the methods described in Shigesada and Kawasaki (1997) D can be estimated as the mean square displacement by an individual's random walk during time t divided by $4t$. In the case of *H. pilosella* the mean square displacement was determined using the mean square daughter distance derived from each of the two years data from the control plots of the

Mt. John study. The intrinsic rate of increase was estimated using the Ricker model described in section 5.2.3.

5.3 Results

In the following results, the values given for all spatial models are derived from the mean of 100 model simulations unless otherwise indicated.

5.3.1 Spatial cellular automata models

Because of the lack of density-dependent mortality, the Wolds CA model suggested that the population would eventually fill 100% of cells. Starting the model with 50 randomly placed rosettes, or 2% of cells filled, the population rose sigmoidally for the first 100 years, but after reaching an apparent asymptote of 85% of the cells filled (Figure 5.2) it continued to rise much more gradually to eventually fill all of the cells. This final steady state was verified by starting the model with 100% of the cells filled, after which no decrease occurred.

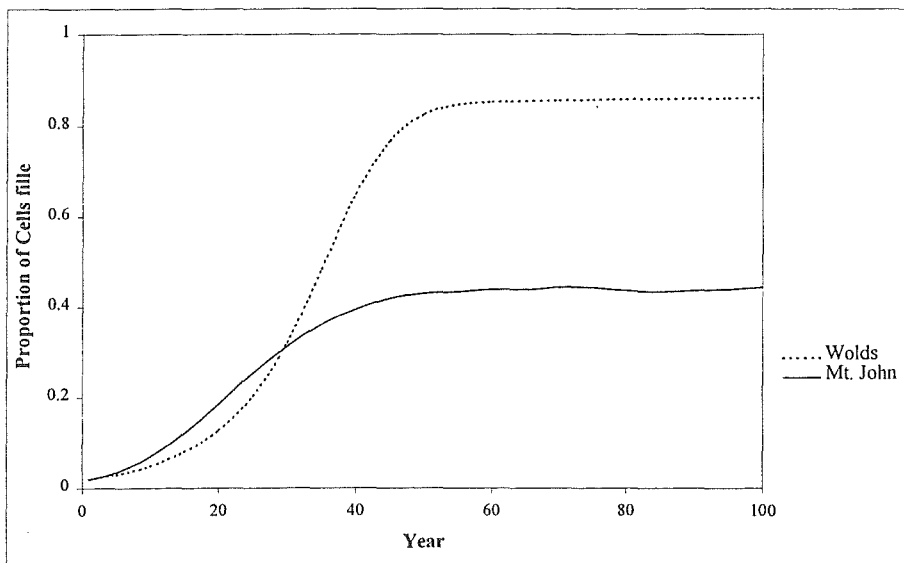
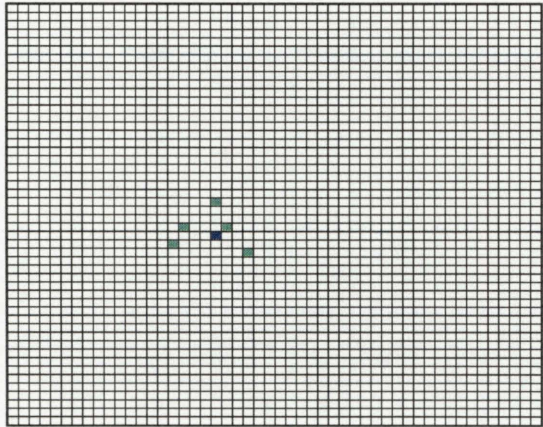
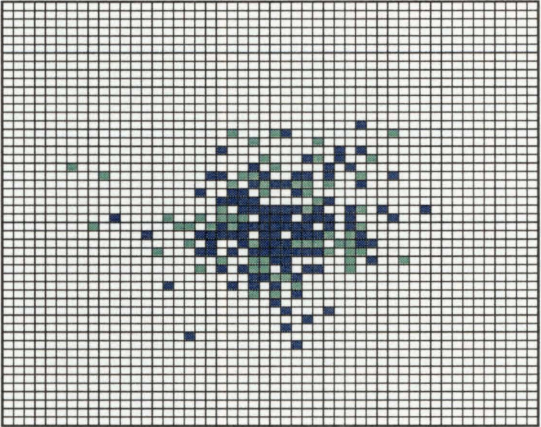


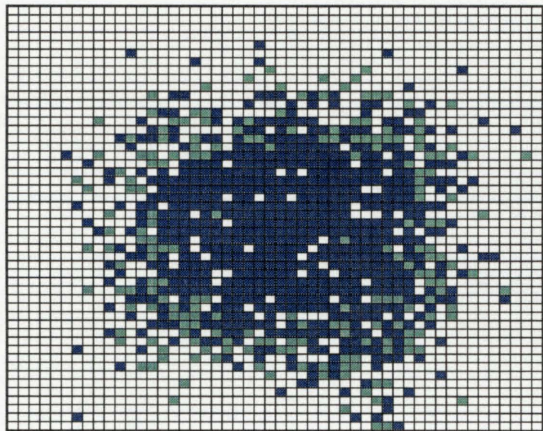
Figure 5.2 Average proportion of available cells filled in 100 simulations of the cellular automata models for Mt. John (Chapter 2) and Wolds (Makepeace 1980). Grid size was 50 x 50 with an initial random seeding of 50 cells.



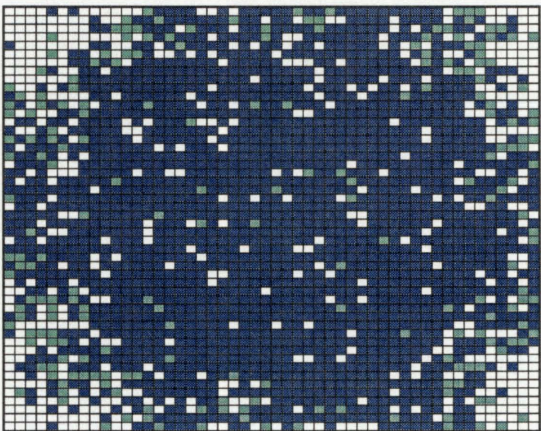
(a) 20 years. Relative density = 0.2%.



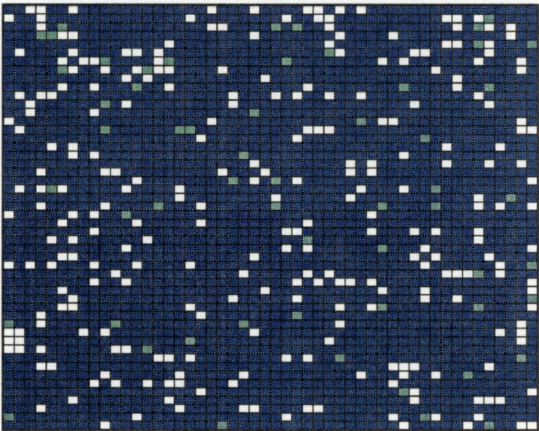
(b) 50 years. Relative density = 7.0%.



(c) 75 years. Relative density = 33.1%.

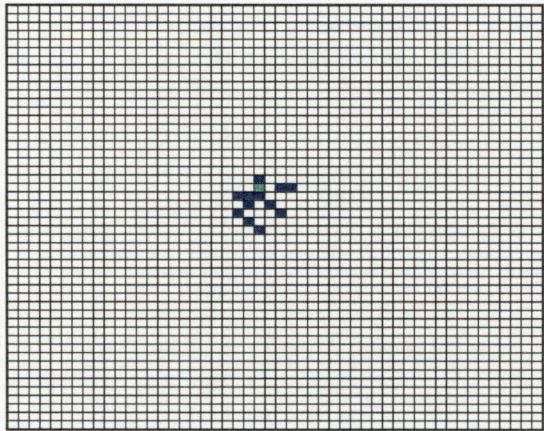


(d) 100 years. Relative density = 78.5%.

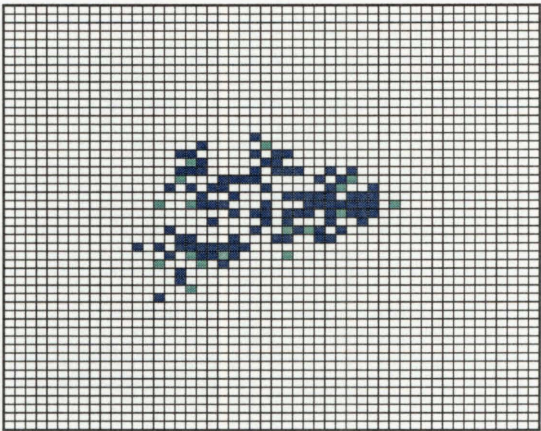


(e) 150 years. Relative density = 88.8%.

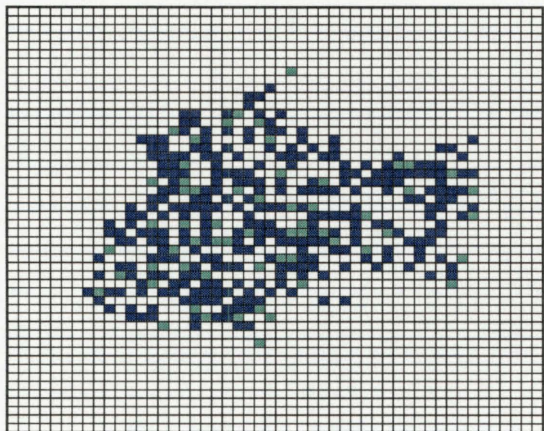
Figure 5.3 Typical simulation of the Wolds cellular automaton model depicting different stages in patch spread. Grid size was 50 x 50 with an initial seeding (year = 0) of the central grid cell. Relative density is the percentage of filled cells. White cells are empty, blue cells are rosettes and green cells are daughter rosettes.



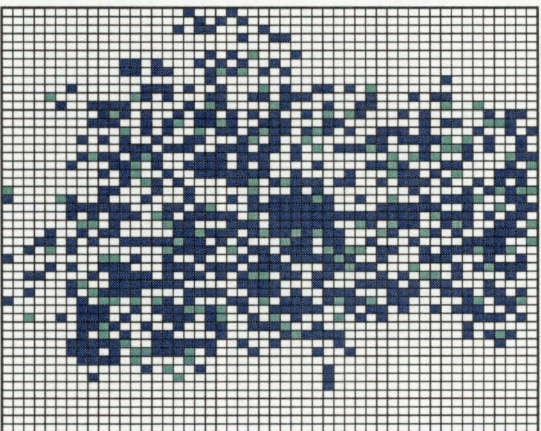
(a) 20 years. Relative density = 0.5%.



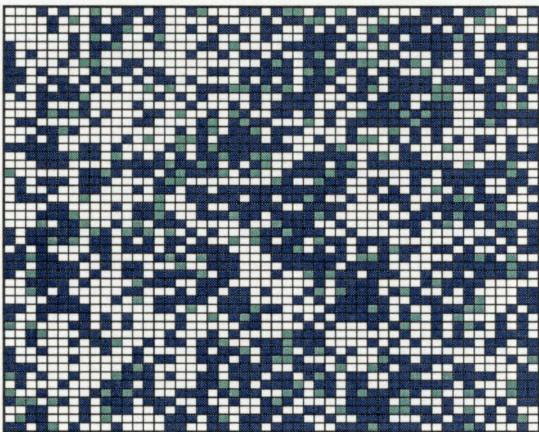
(b) 50 years. Relative density = 4.6%.



(c) 75 years. Relative density = 13.9%.



(d) 100 years. Relative density = 29.7%.



(e) 150 years. Relative density = 52.3%.

Figure 5.4 Typical simulation of the Mt. John cellular automaton model depicting different stages in patch spread. Grid size was 50 x 50 with an initial seeding (year = 0) of the central grid cell. Relative density is the percentage of filled cells. White cells are empty, blue cells are rosettes and green cells are daughter rosettes.

Starting with a single rosette in the centre of the model grid, variation between patch interior and patch edge became evident as a patch spread. During the first 20 years density remained relatively low (Figure 5.3a), with the first 10 years showing little if any spread. After 20 years the patch began to increase in size and between 50 and 75 years the central region filled in (Figure 5.3b, c). Reproduction in the central region then became rare while the patch edge continued to expand outwards (Figure 5.3d).

The dynamics of the Mt. John CA model were quite different from those of the Wolds CA model. The initial spread into vacant cells was slightly faster for the first 30 years and then the rate of spread reduced. A maximum population equivalent to 45% occupation of the available cells was reached after approximately 45 years (Figure 5.2). Running the model for a further 100 years had no effect on the final proportion of filled cells.

Patch diameter changed little in the first 20 years (Figure 5.4a) but steadily increased thereafter (Figure 5.4b - d). The density of the central region was lower than in the Wolds CA model simulation (Figure 5.3e c.f. Figure 5.4e).

When comparing patch diameter with time, the two models predicted almost identical rates of spread (Figure 5.5), namely 5.5 mm per year for Wolds and 5.3 mm per year for Mt. John.

5.3.2 Spatial coupled map lattice model

5.3.2.1 *Simulated dynamics of Hieracium pilosella at Mt John*

The coupled map lattice model predicted logistic population growth (Figure 5.6). From an initial population of 5 rosettes the population steadily rose for approximately 25 years and by about 40 years had reached its maximum of 21 rosettes per cell (averaged over all cells). While the number of rosettes per cell was theoretically unbounded, in practice it never exceeded 50 rosettes in any one cell and the overall equilibrium set by density-dependence was 21 rosettes per cell.

Converting density to cover reveals the same logistic curve with the population reaching about 57% maximum cover.

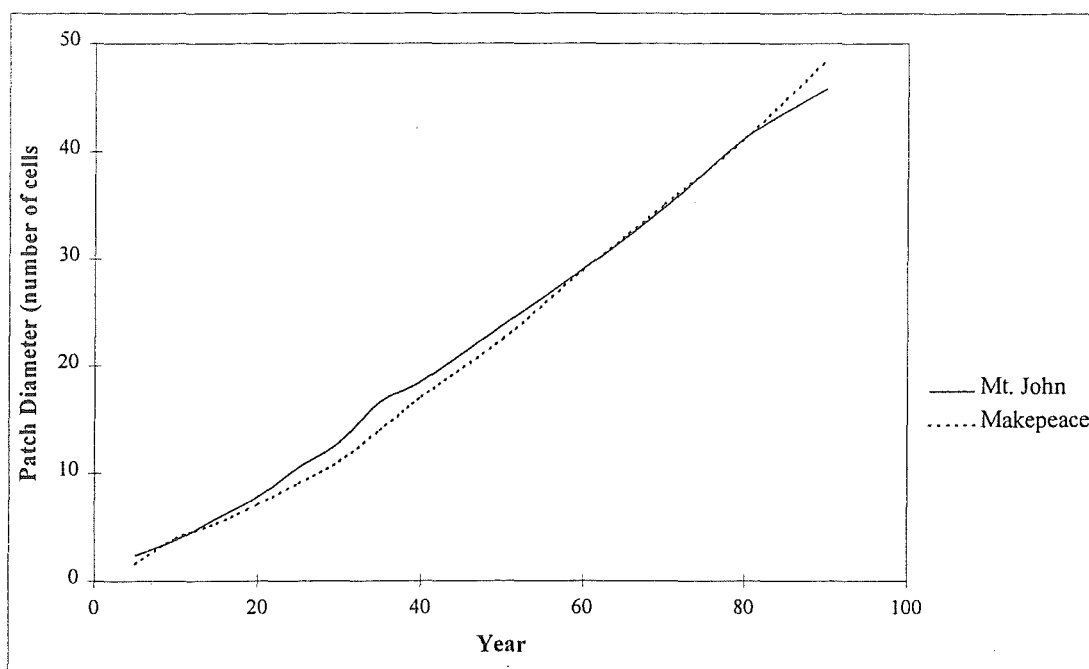


Figure 5.5 Average patch diameter against time for the Mt. John and Wolds cellular automata models started with a single rosette in the central cell. Diameters over 48 cells were ignored to reduce boundary effects.

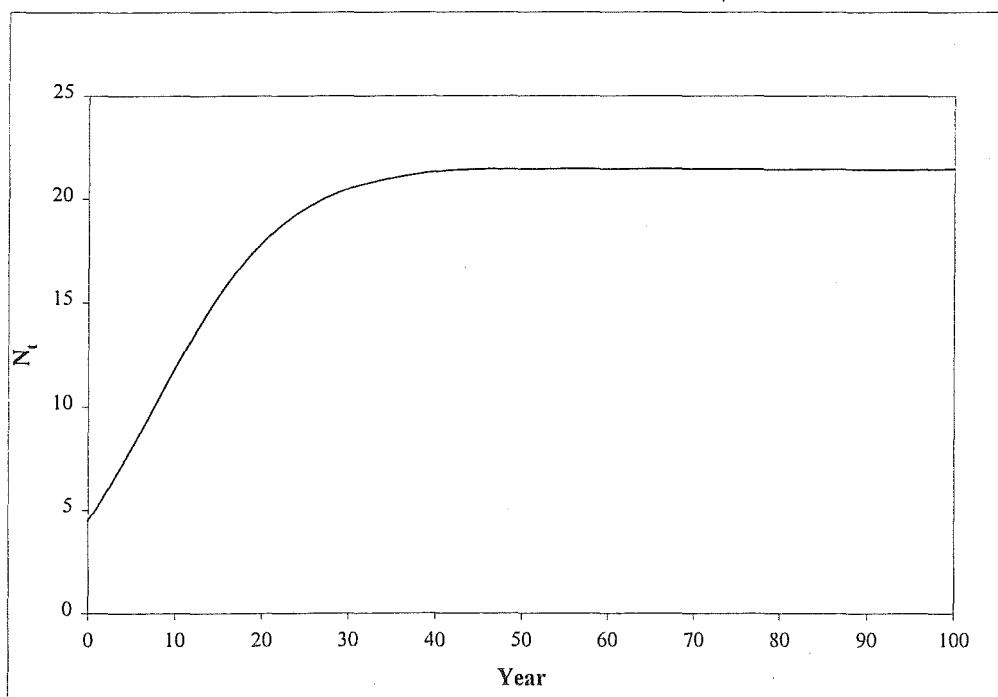


Figure 5.6 Simulated population growth over time (years) of *Hieracium pilosella* in the absence of any control in the coupled map lattice model. Graph depicts the average of 100 model simulations (averaged over all cells) with the initial density in each cell equal to 5 rosettes. Y-axis (N_t) is the average number of rosettes per 49 cm² cell and the x-axis measures time since model initiation.

5.3.2.2 Population spread

Figure 5.7 shows the spread at the front of a clonal group started within a central cell at both low and high densities. While the rate of outward spread varied between 0 and 0.15 cells per year, the average steady state rate of spread, 20 years after model initialisation, was about 0.11 cells per year (approximately 8 mm per year) for both densities. The initial rate of spread was slower for the population started at lower density.

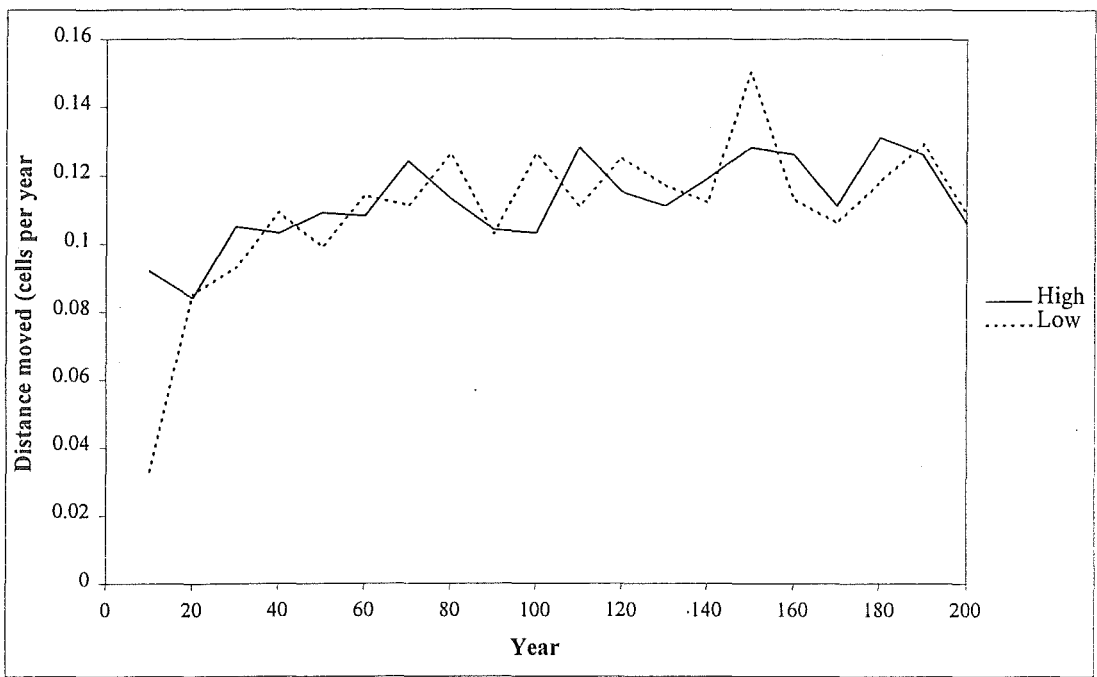


Figure 5.7 The simulated rate of spread at the front of a clonal group started at low and high densities in the coupled map lattice model. Low initial density = 5 rosettes, high initial density = 21 rosettes in the central seed cell. Values are averaged over 100 simulations.

Using the 50% equilibrium isocline rather than the front, the rate of spread was slower when clonal groups were small regardless of the initial density. The average rate of spread tends to about 0.12 cells per year or about 8 mm per year, the same as that for the front (Figure 5.8). After 20 years both initially high- and low-density groups spread at similar rates.

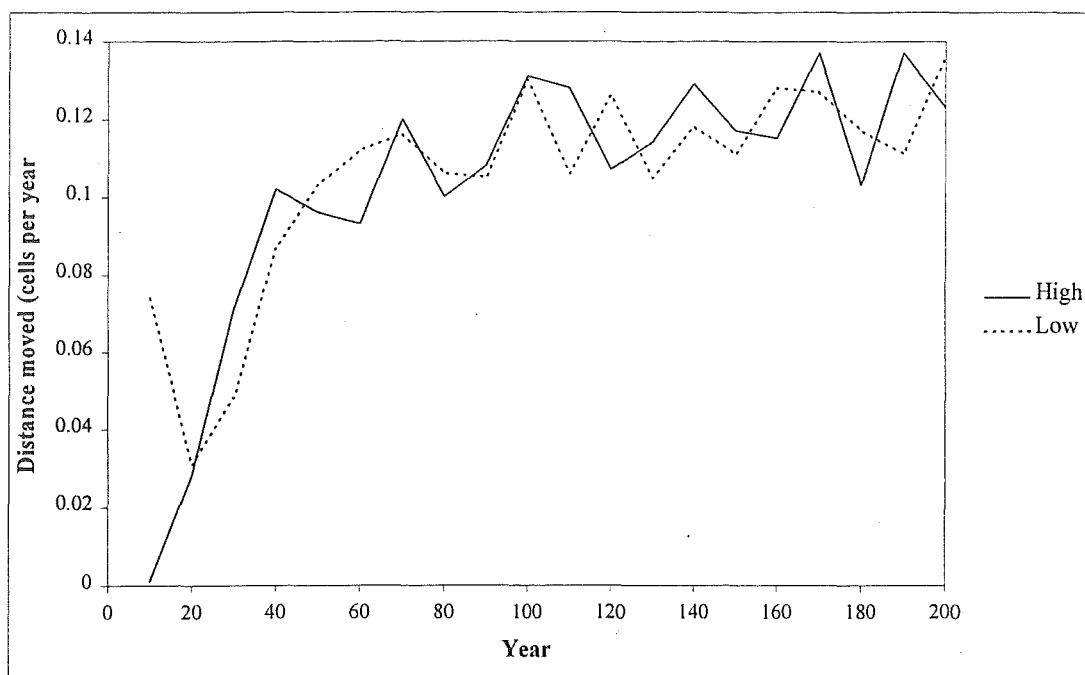


Figure 5.8 The simulated rate of spread of the half steady-state contour for both low (5 rosettes) and high (21 rosettes) densities in the initial seed cell in the coupled map lattice model. Values are averaged over 100 simulations.

5.3.2.3 Effect of treatments

Both fertiliser and water had a substantial effect on the simulated mean rosette density. When both were added to the model, there was a 62% decrease in the steady state of the population, whereas if fertiliser alone was added the population became extinct (Figure 5.9).

With both water and fertiliser added, the cover of *H. pilosella* also decreased 56% initially to approximately 21%, whereas with fertiliser alone the simulation suggested that the cover of *H. pilosella* decreased to extinction in approximately 30 years.

The above results suggest that there was a greater increase in non-reproductive mortality when fertiliser was added, which prompted further exploration of the data collected in the Mt. John field trial. It was found that non-reproductive mortality increased when water was added in the absence of fertiliser but decreased in the presence of fertiliser (Chapter 2 and Table 5.3). In the absence of fertiliser, the effect may be partly due to competition with clover (*Trifolium repens*), which was found to significantly increase with the addition of water (Chapter 2). To test this hypothesis, non-reproductive mortality was

regressed against clover cover and was found to be non-significant ($p = 0.512$). Non-reproductive mortality was then analysed separately in the control plots and water only plots by regressing the two against clover cover. Regression slopes were compared using the methods of Snedecor and Cochran (1980). There was no significant difference between the two slopes suggesting that competition by clover was not the cause for increased non-reproductive mortality.

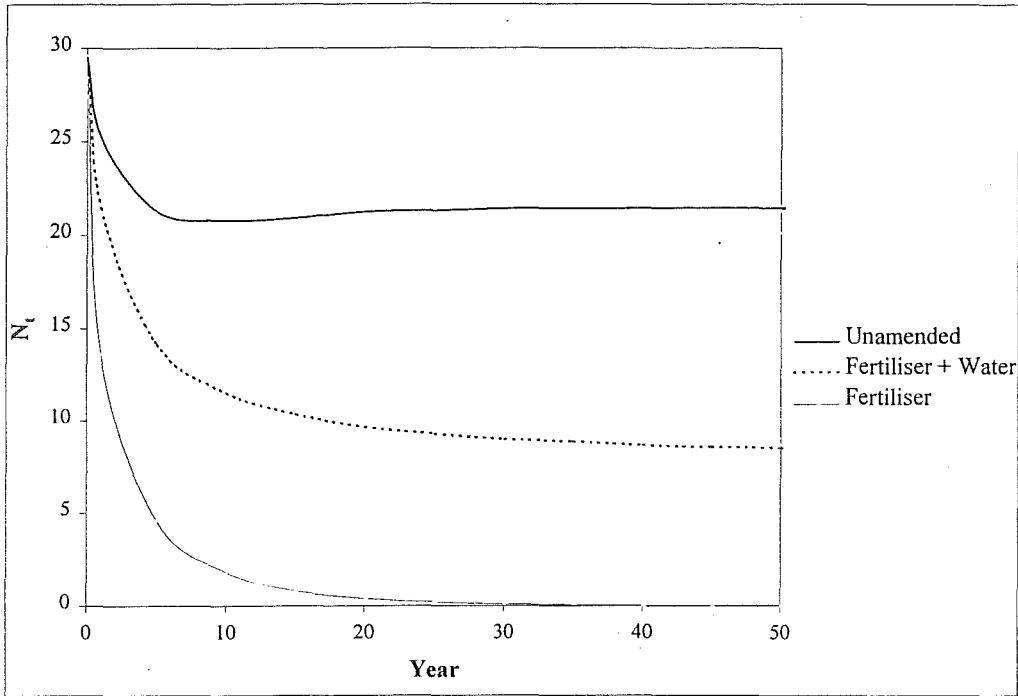


Figure 5.9 The simulated effect of fertiliser and fertiliser + water on the time course of mean population density of *Hieracium pilosella*. Values are averaged over 100 simulations of a coupled map lattice model with initial cell density of 30 rosettes. Y-axis (N_t) is the average number of rosettes per 49 cm² cell and the x-axis measures time since model initiation.

Table 5.3 Mean non-reproductive mortality for *Hieracium pilosella* under the two-way interaction of water and fertiliser ($p = 0.019$). Means are adjusted for the covariate of initial rosette and daughter rosette density and were obtained from ANCOVAs in Chapter 2. Only mean values are presented because standard errors of these treatments are affected by other treatments (i.e. cutting) because of the factorial design of the experiment.

	No fertiliser	Fertiliser
No water	-0.008	0.285
Water	0.180	0.020

Decreased non-reproductive mortality in watered and fertilised plots suggested that fertiliser alone may have been affecting the population, perhaps by causing an increase in death due to root burn or increasing intraspecific competition. To test for a competition effect, non-reproductive mortality was regressed against *H. pilosella* density for plots with fertiliser and no water and plots with fertiliser + water and the regression slopes were analysed as above. Again there was no significant difference between slopes nor were the regression lines significant.

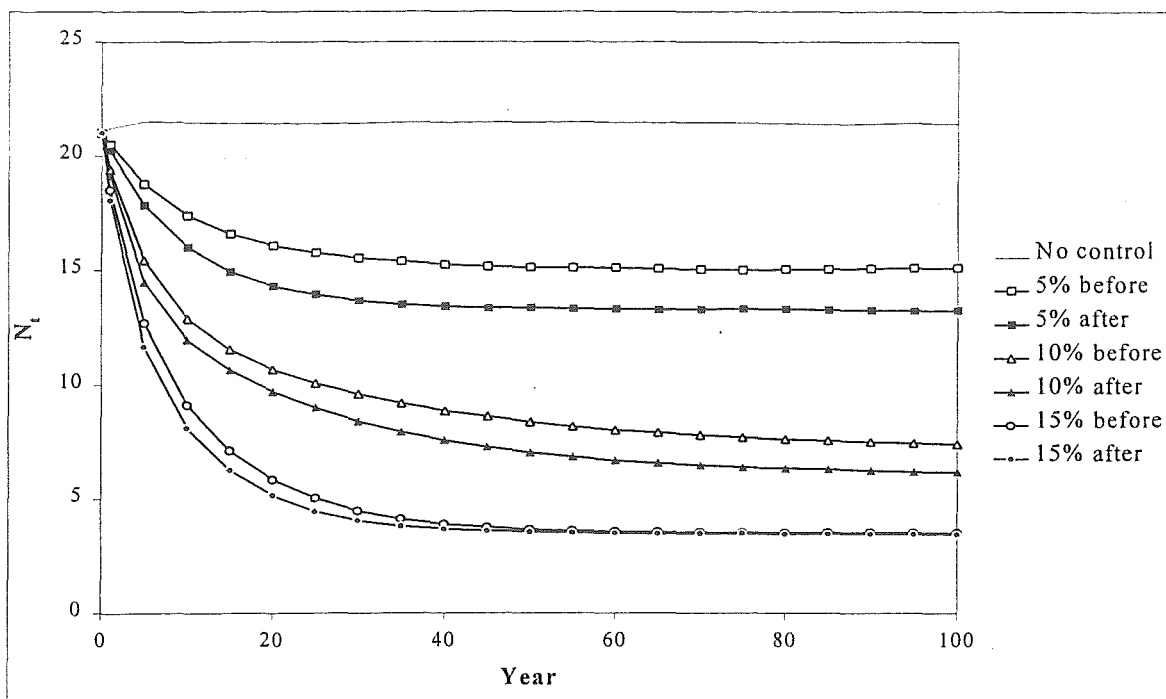
5.3.2.4 *Effect of biological control*

Figure 5.10a and b illustrate the hypothetical effect of biological control on the population density of *H. pilosella*. A control agent which could reduce the population by increasing mortality was far more effective than one which reduced the production of daughter rosettes. When an additional 5 or 10% mortality was added into the model, mortality applied before density-dependent mortality was slightly more effective than that following density-dependent mortality. At greater levels of additional mortality there was little difference in the impact of its timing (Figure 5.10a).

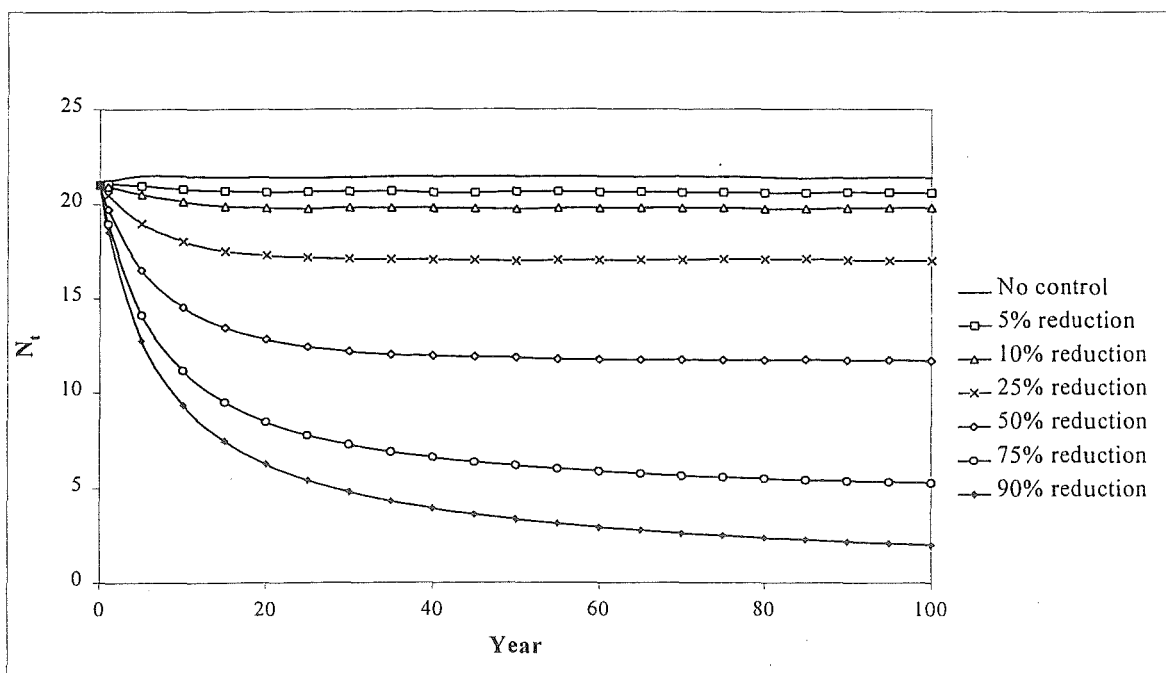
Figure 5.11a shows the simulated effect of continuous increased mortality after 10 years. With an additional 5% mortality and depending on its timing, the population was suppressed by 15% or 21%. Ninety percent suppression required an additional mortality of 30% per year.

Control agents which reduced daughter production had a smaller effect on the population size. After 10 years of control, a 10% reduction in the population would require a decrease in daughter production of more than 20%. A 50% reduction in 10 years would require a decrease of 80% in daughter production (Figure 5.11b).

To reduce the cover of *H. pilosella* to less than 25% from the equilibrium value of 56% a control agent would need to decrease daughter production by about 70% whereas mortality would only have to be increased by approximately 10%. The final steady states for biological control gave slightly higher suppression levels (Figure 5.11c and d) but took significantly longer to achieve (around 50 - 100 years, as in Figure 5.10a and b).



(a) The effect of additional mortality on the population applied either before or after the occurrence of density-dependent mortality.



(b) The effect of reducing the reproductive ability of the population by decreasing the number of daughters per rosette.

Figure 5.10 The simulated effect of a biological control agent on *Hieracium pilosella* in the coupled map lattice model. All model runs were initiated with a density of 21 rosettes in each cell. Y-axis (N_t) is the average number of rosettes per 49 cm² cell and the x-axis measures time since control initiation.

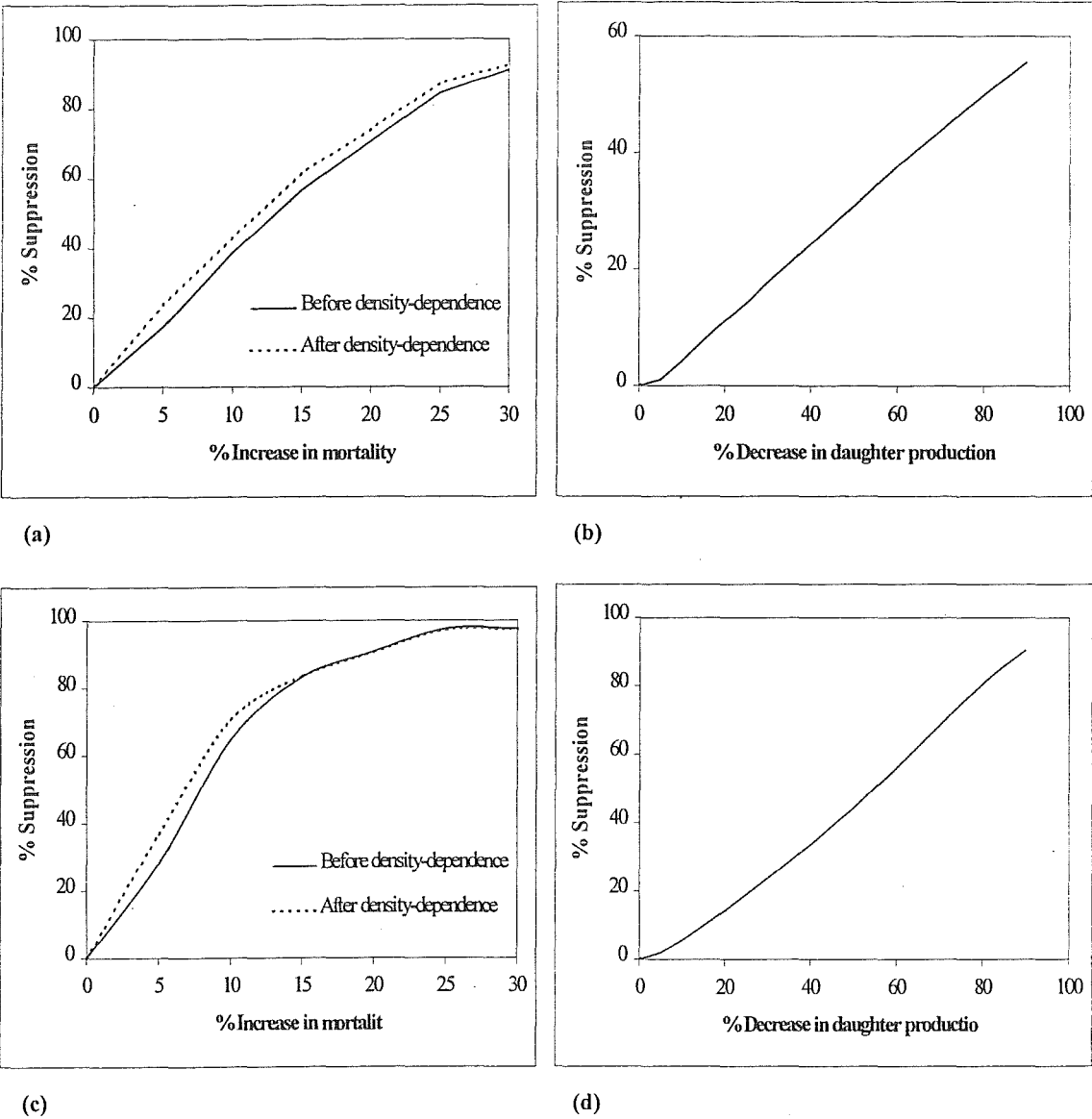


Figure 5.11 Simulated long-term suppression of a population of *Hieracium pilosella* under different levels of biological control. Results are derived from the coupled map lattice model with all cells initialised with 21 rosettes, the model's steady-state. (a) Suppression after 10 years of continuous biological control in the form of either increased mortality applied before/after density-dependent mortality, or (b) decreased daughter production (Note the different range in suppression scale between graphs). (c) Final steady-state suppression levels (after 100 years) for increased mortality and (d) decreased daughter production.

5.3.3 Non-spatial Ricker model

5.3.3.1 Simulated dynamics of *Hieracium pilosella* at Mt John

Results from the discrete Ricker model were similar to those for the stochastic spatial models. In the absence of biological control, the population stabilised at approximately 22 rosettes per 49 cm² (Figure 5.12). Equilibrium density, determined by an interaction

between density-independent reproduction and density-dependent mortality, took about 30 years to occur from an initial density of 1 rosette per 49 cm².

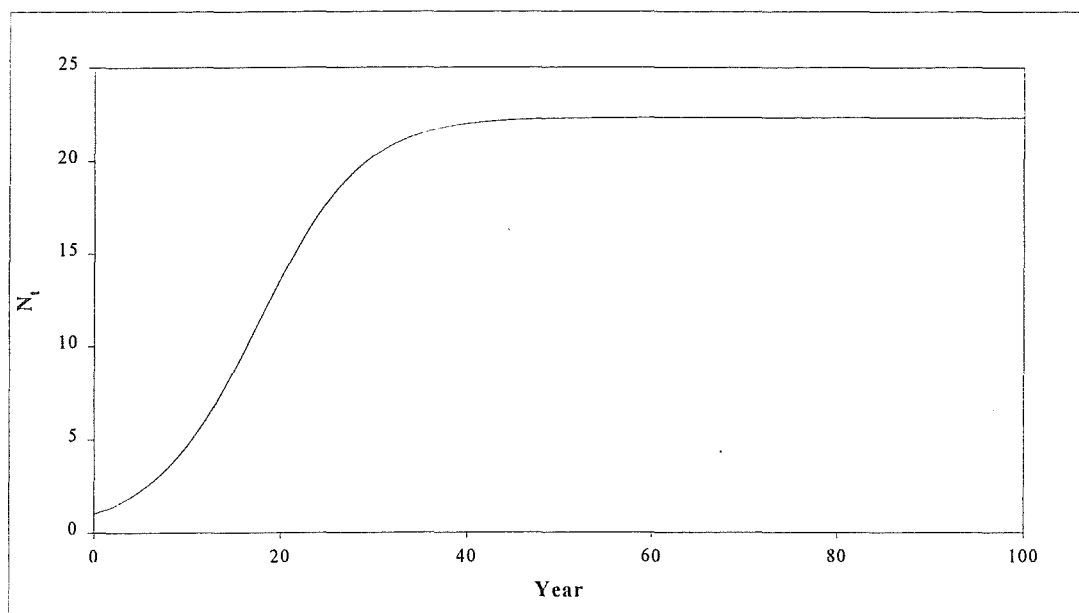
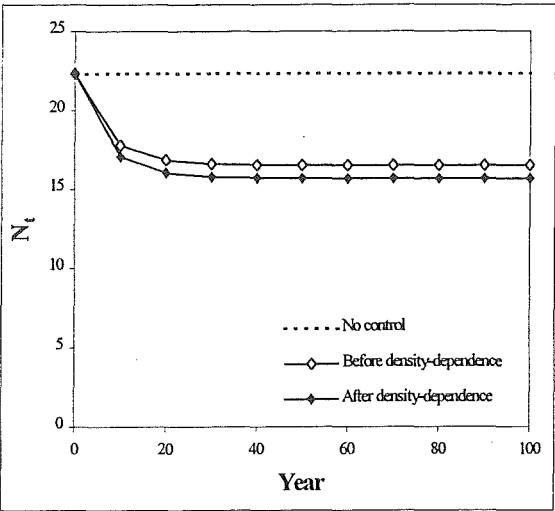


Figure 5.12 Simulated population growth from the Ricker model for *Hieracium pilosella* unchecked by any control agents. The model was initialised with a single rosette. Y-axis (N_t) is rosette density per 49 cm² and x-axis measures time from model initiation.

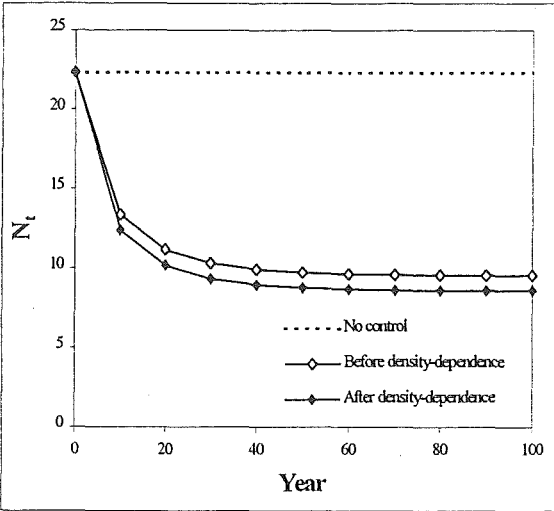
5.3.3.2 Effect of biological control

As in the coupled map lattice model, the difference in timing of additional mortality through biological control was only noticeable when additional mortality was below 15% and suppression levels for given additional mortalities or effects on reproduction rate were the same (Figure 5.13 and Figure 5.14).

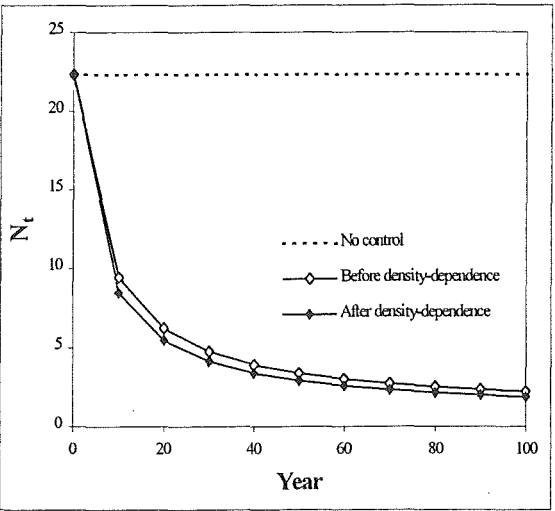
To achieve a 50% decrease in cover within 10 years, a control agent would have to either increase mortality by 13% or decrease daughter production by 80% (Figure 5.15, Figure 5.16).



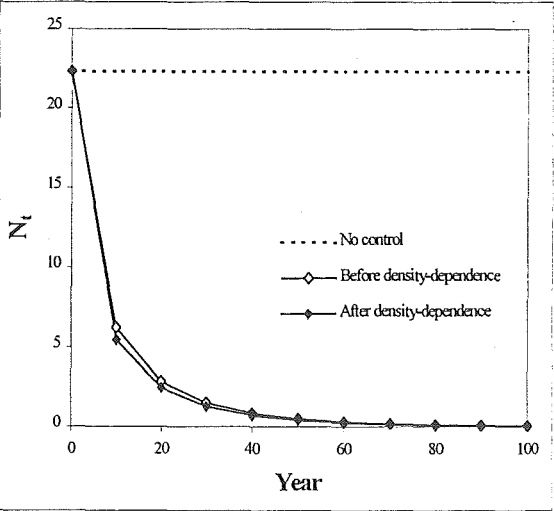
(a) Additional mortality of 5%



(b) Additional Mortality of 10%



(c) Additional mortality of 15%



(d) Additional mortality of 20%

Figure 5.13 The simulated effect of increasing mortality before or after density-dependent mortality in the Ricker model. Y-axis (N_t) is the rosette density per 49 cm² and the x-axis measures time since control initiation.

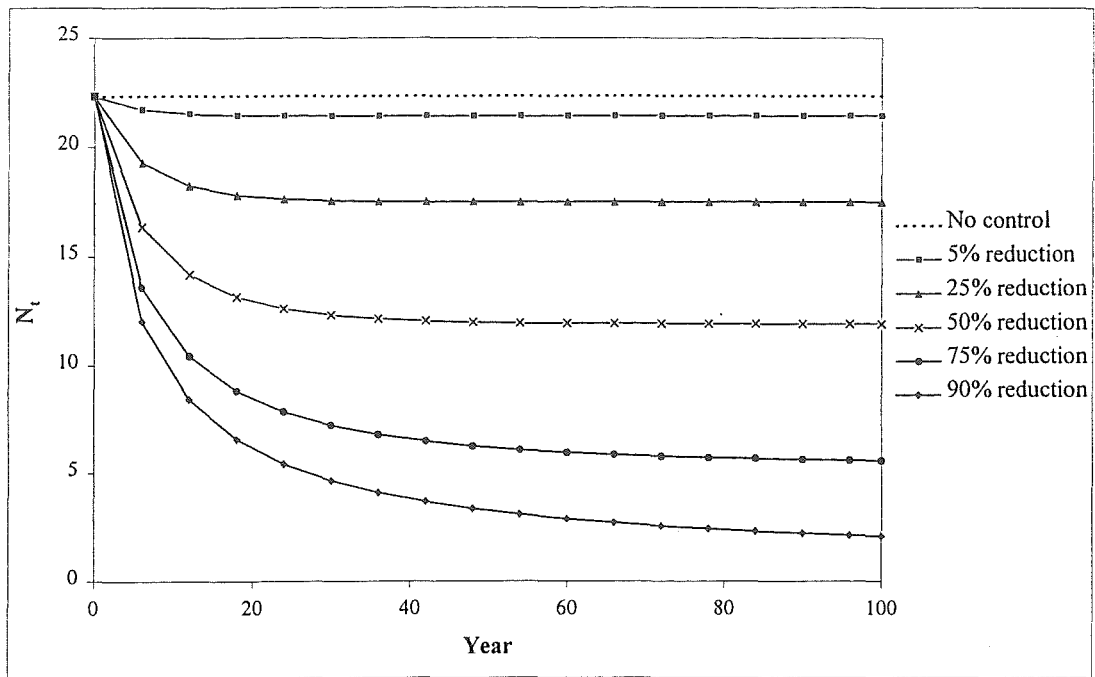


Figure 5.14 The effect of reducing the number of daughters per rosette in a stable population of *Hieracium pilosella*. Results are based on the Ricker model for *H. pilosella*. Y-axis (N_t) is rosette density per 49 cm² and the x-axis measures time since control initiation.

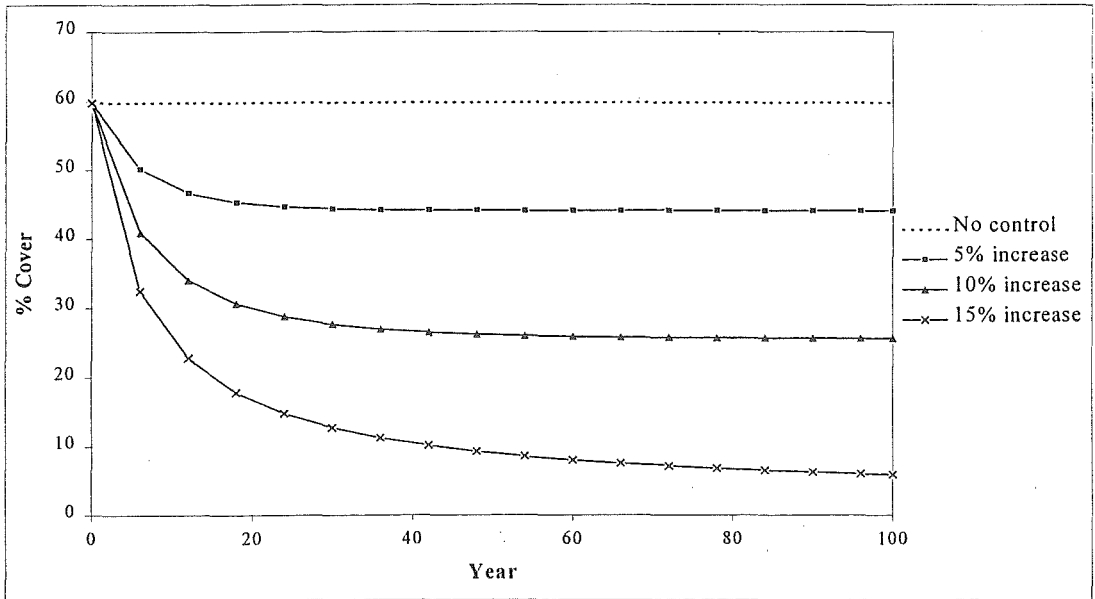


Figure 5.15 The simulated effect of biological control in the form of increased mortality on the total cover of *Hieracium pilosella* from the Ricker model.

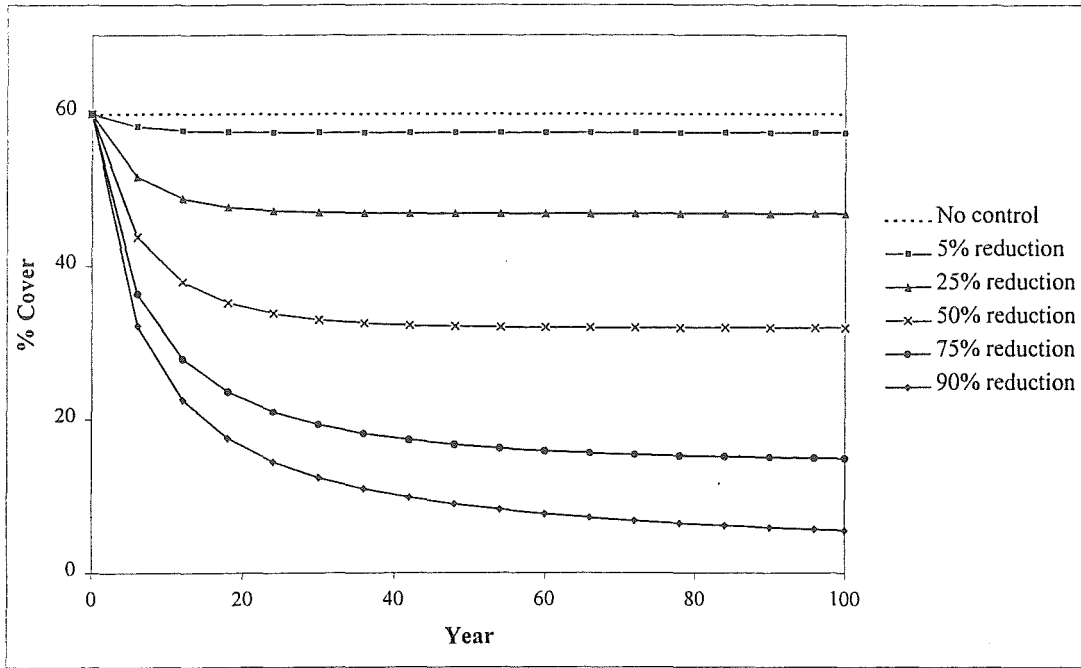


Figure 5.16 The simulated effect of biological control in the form of decreased daughter production on the total cover of *Hieracium pilosella* from the Ricker model.

5.3.3.3 Stability analysis

By examining the stability of a model's equilibrium point(s) one can gain an insight into its behaviour and sensitivity to the different parameters. The same applies to the biological system it represents and management changes like biological control which are superimposed on it. For example if an equilibrium point is unstable, any disturbance in a population may result in a sudden decline in density or the balance between competing groups may shift. If, however, the equilibrium is stable, any disturbance would only slightly affect a system and after a period of time, the population would settle back into its original state. Even simple ecological models, like the Ricker can behave in complex ways depending on its parameter values (May & Oster 1976).

For simplicity, assume that a population can be described by a difference equation of the form:

$$N_{t+1} = F(N_t)$$

Equilibrium in difference equation models occurs at the point where $N_{t+1} = N_t$, say $N^* = F(N^*)$. The stability of this equilibrium point depends on the eigenvalues of F at

N^* (May 1973). Given that the system we are looking at here is a simple single-species population model, the eigenvalues can be found by finding the slope of F at N^* , that is $\left. \frac{dF}{dN} \right|_{N=N^*}$ (May & Oster 1976). If the absolute value of the slope is less than 1, the point is a stable, locally attracting one, if the slope equals 1 the point is neutrally stable and if it is greater than 1 the point becomes unstable tending towards chaos as the slope increases (May & Oster 1976). When a stable point is locally attracting, any small perturbations result in a damping of the population density back to its equilibrium whereas if a point is neutrally stable small oscillations around the equilibrium will persist undamped.

Considering the equations used in this model for *H. pilosella*, the equilibrium points are found by substituting N_t for N_{t+1} into equations (4a), (4b), and (4c) (Section 5.2.3.1).

The following equilibrium points, N^* , emerge:

$$\text{Ricker 1:} \quad N_1^* = \frac{\ln(a(1+R)(1-m))}{b(1+R)(1-m)}, \quad (m \neq 1) \quad (5a)$$

$$\text{Ricker 2:} \quad N_2^* = \frac{\ln(a(1+R)(1-m))}{b(1+R)} \quad (5b)$$

$$\text{Ricker 3:} \quad N_3^* = \frac{\ln(a(1+R(1-m)))}{b(1+R(1-m))}, \quad (m \neq 1) \quad (5c)$$

where a , b and R are defined as in section 5.2.3. Since a , b and R are known and constant, solving these equilibrium equations at $N^* = 0$ for m yields the minimum amount of control required to achieve extinction. Thus for the three models extinction occurs at the following levels of control:

$$\text{Ricker 1:} \quad m_{\min} = \frac{a(1+R)-1}{a(1+R)} = 0.158 \quad (6a)$$

$$\text{Ricker 2:} \quad m_{\min} = \frac{a(1+R)-1}{a(1+R)} = 0.158 \quad (6b)$$

$$\text{Ricker 3:} \quad m_{\min} = \frac{a(1+R)-1}{aR} = 0.938 \quad (6c)$$

Given these minimum values we see that m is bounded below by 0 (i.e. no biological control) and above by m_{\min} , thus stability analyses needs only to include those values of m which fall in that range.

Considering the original model equations, (4a), (4b) and (4c), and determining their derivatives at equilibrium (equations 5a, 5b and 5c) yields the following slopes at equilibrium:

$$\text{Ricker 1:} \quad \text{Slope}_1 = 1 - \ln(a) - \ln(1 - m) - \ln(1 + R) \quad (7a)$$

$$\text{Ricker 2:} \quad \text{Slope}_2 = 1 - \ln(a) - \ln(1 - m) - \ln(1 + R) \quad (7b)$$

$$\text{Ricker 3:} \quad \text{Slope}_3 = 1 - \ln(a) - \ln(1 + R(1 - m)) \quad (7c)$$

In order for the N^* s to be stable equilibrium points, the absolute value of these slopes must be less than 1 and thus, m must be bounded as follows:

$$\text{Ricker 1:} \quad \frac{a(1 + R) - e^2}{a(1 + R)} \leq m \leq \frac{a(1 + R) - 1}{a(1 + R)} \quad (8a)$$

$$\text{Ricker 2:} \quad \frac{a(1 + R) - e^2}{a(1 + R)} \leq m \leq \frac{a(1 + R) - 1}{a(1 + R)} \quad (8b)$$

$$\text{Ricker 3:} \quad \frac{a(1 + R) - e^2}{aR} \leq m \leq \frac{a(1 + R) - 1}{aR} \quad (8c)$$

Again, substituting the values for a and R into equations (8a), (8b) and (8c) yields the values for m in which stability occurs:

$$\text{Ricker 1:} \quad -5.22 \leq m \leq 0.158$$

$$\text{Ricker 2:} \quad -5.22 \leq m \leq 0.158$$

$$\text{Ricker 3:} \quad -31.09 \leq m \leq 0.938$$

Since m is bounded below by 0 then in all cases for values of m below m_{\min} the equilibrium points are stable local attractors. Biologically this means that any small disturbance of a population will have no effect on its final steady state.

5.3.4 Analytical spatial model

The average mean square daughter distance calculated from the original mapping of the Mt. John rosettes was 197.7 mm^2 . This gave a diffusion coefficient (D) of $49.43 \text{ mm}^2/\text{yr}$ ($D = [\text{M.S. daughter distance}]/4$). The intrinsic rate of increase (ϵ) from the Ricker model was 0.17, hence, the velocity of spread ($2\sqrt{\epsilon D}$) was found to be 5.8 mm/yr . This compares with 8.4 mm/yr for the coupled map lattice model and 5.3 mm/yr for the cellular automaton model (although the latter is a minimum estimate owing to each rosette only occupying 1 cm^2).

5.4 Discussion

5.4.1 Population dynamics and patch spread

Individual-based plant population models use two general approaches to represent spatial location and interaction of individuals. The first subdivides space into discrete cells in which each cell usually represents a single plant (Barkham & Hance 1982; van Tongeren & Prentice 1986; Crawley & May 1987; Hobbs & Hobbs 1987; Green 1989). The second approach depicts each plant as a single point on a modelled spatial plane (Pacala & Silander 1985 & 1990; Pacala 1986a, 1986b & 1987; Czárán & Bartha 1989; Cain *et al.* 1995). One of the main differences between the two types of models is that in the model which divides space into discrete cells there is an imposed rigid density-dependence as each cell can hold a maximum of only one plant. In a sense, the carrying capacity of the model space is bounded above by the grid size and once all the cells are filled there can be no recruitment until a cell becomes vacant. In contrast, when each cell is allowed to hold a population of plants or plants are depicted as points on a plane, there could conceivably be an infinite population density thus eliminating a model-imposed density-dependence. To examine the possible limitations of the two approaches, both alternatives were adopted here, with either a single plant per cell (cellular automaton) or a population of plants per cell (coupled map lattice). There was close agreement between the results of the two models, which suggests that the results are not artefacts of the precise model structure chosen.

The cellular automaton model based on the variation in vital rates found within patches of *Hieracium pilosella* at Wolds (Makepeace 1980) gives different results from the model

developed using data from the Mt. John population. The proportion of cells occupied during the first 30 years of simulation was greater for Mt. John than Wolds. After this time, the Mt. John population stabilised at about 45% occupancy whereas the Wolds population continued to increase to 85% occupancy. Given enough time, the Wolds CA model could achieve 100% occupancy. The difference was due to the density-dependent mortality in the Mt. John CA model, which was absent in the Wolds CA model. The steady-state density in the former model of 21 rosettes per 49 cm² area is equivalent to 45% cell occupancy. The Wolds CA model gave a relatively rapid increase in occupancy to 85% because patch edges still would have been present and those rosettes on the edges would have been reproducing at a higher rate. Once the edges disappeared, rosettes were still able to reproduce although the number of daughters would have been greatly reduced, hence the subsequently slower rise to 100% occupancy. There was no non-reproductive mortality constraining the population's increase in the Wolds CA model.

These differences are partly due to the populations from which the data were collected, particularly the lack of density-dependent mortality in the Wolds CA model. Makepeace (1980) purposely chose areas with discernible patches for his study of zonal variation whereas such patches do not exist at Mt. John. It is possible that the two models depict two different stages in *H. pilosella* invasion: an early expanding phase and a mature or senescent phase. In the early phase, the spread of patches is enhanced by high reproductive rates of rosettes at their edges. Effectively the reproductive rate is density-dependent because rosettes have fewer neighbours on patch edges as compared to patch interiors. Given enough time and under the right conditions, the population would be able to occupy all of the available space. However, as patches expand, the population becomes limited in its ability to spread because the overall ratio of patch edges to patch interiors declines as the patches coalesce. Limitations may include competition for space, light or nutrients or it may be a residual effect of *H. pilosella* depleting or otherwise rendering adverse its own environment. Regardless of causes of limitation, once the population reaches the point where there is a shortage of some requirement, reproduction ceases to be the prime regulatory force and density-dependent mortality takes its place, as seen at Mt. John. Patches begin to thin and the population is unable to occupy 100% of the available space. As bare ground increases there may be an opportunity for other species to enter into the system. In Breckland, this pattern was

observed with *Festuca ovina* being replaced by *H. pilosella* which was later replaced by *Thymus* spp. (Watt 1962 & 1981).

It seemed surprising that Makepeace found no evidence for non-reproductive mortality of rosettes, particularly in patch interiors. A possible reason was the length of Makepeace's study. There was no final population census during the spring following the trial, which might have shown extra mortality. At Mt. John, the majority of non-reproductive mortality occurred between May and October with summer mortality mostly limited to reproduction.

The coupled map lattice model suggests that the steady-state density for the population at Mt. John is 21 rosettes per 49 cm² or approximately 4300 rosettes per m². Other studies have found that *H. pilosella* density can vary from a few to over 4500 rosettes per m² (Bishop *et al.* 1978; Widera 1978; Makepeace 1980; Bishop & Davy 1984; Davy & Bishop 1984) with most falling between 1000 and 3000 rosettes per m². The estimated current density at Mt. John is approximately 3200 rosettes per m² suggesting that the population has the ability to increase. This study (Chapter 2) found that the density had increased slightly (3% per year) over two years in the control plots but this increase was slower than the model predicted, suggesting that the model is overestimating the steady-state density. This may be due to other factors which become more important as densities increase, such as competition from the few other plants present, or higher drought stress. In other words, there may be stronger density-dependent mortality when densities reach >4000 rosettes per m² that may not be evident in the few available sample plots from Mt. John.

The rate of spread of patches was determined to be less than 1 cm per year for all models. This is in contrast to the average of 13 cm found by McIntosh *et al.* (1995). One reason for the difference is probably their deliberate selection of small patches (< 1.5 m in diameter) without senescent centres for their sample set. Another reason may be that the Mt. John models are based on a mature population. The difference in the rate of spread between the model patches and those studied by McIntosh *et al.* certainly concords with the hypothesis suggested above, that *H. pilosella* populations go through a growing and then a senescent phase.

The rate of patch spread for the explicit and analytical spatial models were similar although the rate for the coupled map lattice model was slightly higher.

5.4.2 Population control

The coupled map lattice and Ricker models verify the findings of other researchers in suggesting that application of fertiliser is one way of controlling *H. pilosella* (Davy & Bishop 1984; Scott *et al.* 1990a; Svavarsdóttir 1995). The addition of fertiliser alone caused a dramatic decrease in the model population within the first five years and with continued application of fertiliser the model population went extinct within 30 years. Field observations suggest that this decrease in the density of *H. pilosella* is in response to increased competition with other species (Davy & Bishop 1984; Svavarsdóttir 1995). However, the analysis presented in section 5.3.2.3 suggest either that competition is working in ways too subtle to detect with these simple methods, or that there are reasons other than competition that explain the observed decrease in density.

The addition of water and fertiliser together helped to control the model population but did not have as great an effect as fertiliser on its own. Instead of elimination, there was a predicted decrease in the steady-state density of 62%. The reason for this difference is not clear but analysis suggests that the lower steady-state density under the fertiliser-only treatment is due to an increase in non-reproductive mortality compared to the water + fertiliser treatment. This increase in non-reproductive mortality may be due either to the increase in competition between *H. pilosella* rosettes or to an effect such as root burning when fertiliser was added in the absence of water. Both of these theories would have to be studied further before drawing definitive conclusions. Whatever the mechanism, the results may have strong implications for the control of *H. pilosella* by the application of fertiliser in moister areas.

The models suggest that the best form of biological control would be an agent which was able to increase the mortality rate of rosettes and daughters. An agent such as *Aulacidea subterminalis* which forms galls in the stolons of *H. pilosella* would have little effect on the overall density of the population unless it was able to reduce the number of daughters produced by at least 50%, even at low *H. pilosella* density. In addition, considering that 48% of the daughters produced in the Mt. John study and 95% of the daughters produced

in the central patch zone in Makepeace's study were axillary (i.e. had a stolon length of 0), this type of control agent would be unlikely to succeed on its own. If, on the other hand, it was possible to find a control agent that was able to increase rosette mortality by 5 to 10% then the chances of achieving an acceptable decrease in the population density may be quite high.

To date, few, if any, population models have been developed for weedy clonal species and the number for other non-clonal weedy species is minimal, when compared to models applied to host/parasitoid systems for example. The majority of these plant models concentrate on the population dynamics of a seed producing plant and model biological control as an additional mortality. Although useful, this does not allow predictions to be made about the control agent's ability to sustain control under different pest population densities.

Several models of weedy, seed producing plant species have shown that biological control agents affecting fecundity by reducing seed production would have to achieve a reduction of over 95% to lower the plant's density to some "acceptable" level (Cloutier & Watson 1989; Hoffmann 1990; Smith, Holt & Webb 1993; Lonsdale, Farrell & Wilson 1995 but c.f. Shea & Kelly in press). Of these studies, one suggested that the required 99.5% control of seed production from *Centaurea diffusa* could be reduced to 94% if an additional agent were released which could decrease seedling establishment by 90% (Cloutier & Watson 1989). In a model of *Sesbania punicea*, a weedy shrub in South Africa, a 99% reduction in seed production was required before plant densities were deemed suitably low, but only a 10 - 50% increase in plant mortality was required to achieve the same density. With both forms of control combined, the model predicted rapid decreases in the population size with only a 75% reduction in seed (Hoffmann 1990). These results are typical of systems in which density-dependence acts on reproduction (Barlow in press). However, Shea and Kelly (in press) calculated in *Carduus nutans* that seed predation of ca 70% would be sufficient for biological control to succeed. Given the lack of density-dependent regulation in the vegetative reproduction of *H. pilosella* at Mt. John, small increases in mortality of rosettes had a great effect on the population. However, because mortality was density-dependent, decreases in daughter production were met with decreases in mortality resulting in only slight

decreases in overall population density. Hence, daughter production had to be reduced by considerable amounts before the density was decreased by 50%.

The effect of the timing of biological control relative to that of density-dependence has not been explored in other weed biological control models, but in host/parasitoid models, the timing of biological control can have a considerable influence on the success of a control agent (May *et al.* 1981). In the present case, the timing of additional mortality due to biological control with respect to density-dependent mortality had little effect, mainly because of the low magnitude of density-dependence (May *et al.* 1981). When a better understanding of the dynamics of potential control agents is achieved (e.g. dispersal behaviour, rate of increase, searching ability), it may be necessary to re-analyse the effects of density-dependent mortality on the plant and the agents' impact on the population. However, such understanding may be difficult to obtain in practice, since it can only come from post-release field studies.

5.4.3 Model comparison

An extensive search of the literature suggests that examples of comparisons of spatial models with non-spatial models do not exist, suggesting that this is the first study to make such a comparison. In this study, the spatial simulations (cellular automaton and coupled map lattice models), spatial diffusion model and discrete Ricker model for the population of *H. pilosella* at Mt. John gave similar results. This increases confidence that each model was behaving in a plausible way. In addition, the simple and detailed models provide, on the one hand, a succinct portrayal of the system and its responses to management, and on the other, a basis for spatially explicit models which include other factors like interspecific competition, possibly dependent on spatially heterogeneous nutrient profiles.

5.5 Conclusions

Simple models are useful tools in focusing research effort on critical components of a plant's population dynamics. They are also effective devices for assisting in the selection of appropriate biological control agents.

Comparison of models for *Hieracium pilosella* populations at Mt. John and Wolds, suggests that the dynamics of the populations at the two sites were different. The Wolds data were collected from a population in which discernible patches were still present and spreading. In these patches, reproductive rates varied between patch interiors and edges and mortality was restricted to reproductive rosettes. The study only spanned part of a year however, so non-reproductive mortality over the winter period would not have been detected. In contrast, the population at Mt. John is mature and individual patches no longer exist. In this population, it was found that the regulating force was density-dependent mortality (largely over winter) rather than reproduction.

Given the differences of the populations studied, the cellular automata models are best viewed as depicting two different stages in *H. pilosella* invasion. The models suggested that in the early phases of invasion a population either has the potential to occupy 100% of available space, or the forces which will ultimately prevent it from occupying 100% of the space are not yet evident because too little space is currently occupied. After this colonising phase, the population becomes limited in its ability to spread. Density-dependent mortality becomes the regulating force, patches begin to thin and the population is no longer able to occupy all available space.

In addition to the two simulation models (cellular automata and coupled map lattice), simple models were developed which summarised *H. pilosella* dynamics temporally and spatially. These were respectively, the Ricker model for density-dependent growth:

$$N_{t+1} = 1.19N_t e^{-0.012N_t}$$

and the two-dimensional Fisher diffusion model for density-dependent growth and spatial spread:

$$\frac{\partial n}{\partial t} = 49.43 \left(\frac{\partial^2 n}{\partial x^2} + \frac{\partial^2 n}{\partial y^2} \right) + (0.17 - 0.42n)n$$

The spread of model patches was estimated to be less than 1 cm per year with the coupled map lattice model giving the fastest value (8.4 mm/year). In general, the spatial models' rates of spread were similar to that derived from Fisher's diffusion model.

Both the coupled map lattice and Ricker models developed for Mt. John populations of *H. pilosella* suggest that the best form of biological control would be an agent that increased the mortality of a population rather than decreased its fecundity. The models assume that the control agent would be able to cause the same amount of damage each year regardless of *H. pilosella* density. This is obviously an oversimplification but in the short term provides useful guidance for selection of agents, their likely maximum impact on plant population density, and the further study needed to develop more accurate models.

6. Conclusions

6.1 Concluding Discussion

6.1.1 Context of thesis

The infestation of much of New Zealand's high-country by *Hieracium pilosella* has caused general concern for the economic and environmental value of these lands. While there have been several studies of *H. pilosella* in New Zealand, there has been no analysis of its population dynamics. Most previous work has focused on changes in rank, frequency or cover over time (Scott *et al.* 1990a & 1990b; Treskonova 1991a; MAF 1992, 1993, 1994 & 1995; Scott & Sutherland 1993; Espie 1994; Rose *et al.* 1995) while others have investigated differences in nutrients in *Hieracium* and non-*Hieracium* soils (McIntosh & Allen 1993; McIntosh *et al.* 1995; Espie & Boswell Submitted). One study, carried out nearly 20 years ago, attempted to explain the demography of *H. pilosella* populations (Makepeace 1980), but considered only part of a year; it did not encompass overwinter mortality or the demography in mature stands. The present study aimed to provide a more complete understanding of population dynamics, including sources of regulation. It focused on an area which has had *H. pilosella* as the dominant component of the plant community for 3 or more decades, and used as its framework the development of population models together with an extensive set of field trials to provide necessary and currently unavailable data. The models allowed predictions of rates of spatial spread, changes in density and, most important, the likely impact of biological control on *H. pilosella* populations, which is one of the few feasible options for managing this weed.

6.1.2 Ecology of *Hieracium pilosella*

This study of a mature population of *H. pilosella* in a South Island high-country region at Mt. John suggests that the population is regulated by mortality rather than reproduction, with both total mortality (reproductive and non-reproductive) and non-reproductive mortality being density-dependent. In addition, a link was found between reproductive vigour and rosette size or age, although there seemed to be no change in the reproductive threshold size with respect to age. Both in the glasshouse and the field, only the largest rosettes reproduced, suggesting that those rosettes which were better able to capture resources would contribute the most to the continuation of the population. This

observation, combined with the finding that young rosettes (including daughter rosettes) were more likely to reproduce, suggests that once a rosette reaches a certain age it no longer contributes to the maintenance of the population and may aid in the population's demise by increasing intraspecific competition.

6.1.3 Population dynamics of *Hieracium pilosella* in the Mackenzie basin

The population at Mt. John seems to be at or near an equilibrium density of approximately 3200 rosettes per m². This apparent stability may be subject to a longer-term trend due to plant-induced environmental degradation operating on a time scale of decades, since experimental work during this study suggests that *H. pilosella* performs better in soil in which it has not previously grown. The population models developed from data presented in this study suggest that the current Mt. John situation and that in a study carried out nearly 20 years ago at Wolds (Makepeace 1980), are best viewed as depicting two different stages in *H. pilosella* invasion and establishment. During the early stages of invasion, plants are able to exploit available resources, possibly to the detriment of other resident species, to achieve high densities and occupy 100% of available space. Once these high densities are achieved, the local environment becomes degraded through nutrient depletion or presumed allelopathic effects, reproductive rates decline and density-dependent mortality regulates rosette numbers. As a result, the age structure of the population becomes older through lack of recruitment, which in turn accentuates a decline in reproduction since older plants have a lower reproductive rate. The population is no longer able to occupy all the available space, patches begin to thin and areas of bare ground are exposed. The lack of colonisation of the bare areas by other plant species may be attributable to the same factors which limit *H. pilosella*'s own performance in soils where it has previously grown.

For both the Mt. John and Wolds scenarios the models predicted the spatial spread of populations to be less than 1 cm/yr. However, other studies indicate that patches which are still in the expanding phase can increase in diameter by 14 cm/yr (McIntosh *et al.* 1995) suggesting that, for reasons not currently clear, higher rates of spread may be possible than those prevailing both at Wolds and Mt. John.

6.1.4 Management

The Mt. John situation appears to represent a steady state, and to change it would require a significant change in management practices. The addition of water and/or fertiliser greatly increased daughter rosette production, stolon production and stolon length. This increase in reproductive vigour was paralleled by an increase in intraspecific competition, probably for light and space, which resulted in an overall decline in population density but not in cover. The addition of fertiliser and water also caused an increase in other resident species, particularly *Trifolium repens*, and the presence of these competitor species may contribute to the *H. pilosella* decline. However, Svavarsdóttir (1995) suggested that fertiliser may favour *H. pilosella* and, unless continuously applied in adequate amounts, can lead to a decrease of desirable species through resource limitation. While fertilising and oversowing have proven to be effective in many areas, they require constant input which is unlikely to be sustainable in the long term. This method of control is often uneconomical on low-value pastures and is inappropriate for regions with high conservation values.

There was little effect of simulated grazing on *H. pilosella* dynamics apart from an increase in the proportion of rosettes producing stolons and the expected decrease in flowering success. There was no increase in stolon length or daughter production, therefore supporting the suggestion by Scott *et al.* (1990a) that grazing alone is ineffective in controlling *Hieracium* infestations.

6.1.5 Implications for biological control

At first sight, an agent which could successfully reduce the production of daughter rosettes would seem a promising candidate for biological control. Not only would the agent reduce the numbers of recruits into the population, but because *H. pilosella* is monocarpic, it would also allow mortality associated with reproduction to be maintained. This may be effective in slowing or stopping the spread of *H. pilosella* in areas in which it is still expanding and not regulated by density-dependent mortality. However, in a mature population a reduction in the number of vegetative progeny (unless unrealistically high) would have little effect on the overall population density. Instead, population models suggest that the introduction of an agent which could successfully increase the overall mortality of the population would have a far greater impact on population density.

For example, to reduce the population by 50%, an agent would either have to decrease daughter production by approximately 80% or increase mortality by about 12%.

The economic and environmental impact of a successful biological control agent is difficult to predict, however current studies by Landcare Research suggest that a decrease in *H. pilosella* density allows for an increase in total indigenous vegetation, total exotic vegetation (excluding *H. pilosella*), litter and bare ground (Syrett *et al.* 1996). If significant reductions in *H. pilosella* are achieved, it will be important to monitor the exotic vegetation to ensure that *H. pilosella* is not replaced by another undesirable species.

6.2 Recommendations for Further Research

Based on this study, the following research is recommended to further develop an understanding of *Hieracium pilosella* population dynamics and the likely effect of biological control:

- An investigation as to whether older rosettes have less chance of reproducing at equal size to younger rosettes and an understanding of the general age structure of *H. pilosella* populations. This would help in determining the long-term effect of control agents which reduce the fecundity of the plant.
- An investigation of interactions between *H. pilosella* and other species in the field to determine under what conditions *H. pilosella* can and cannot displace resident species. This would provide the information needed to include competition with other species in the population models as well as providing a better understanding of how *H. pilosella* interacts with other species in the field.
- A more in-depth study of the long-term effects of *H. pilosella* on soil and their implication for the establishment of *H. pilosella* and other species.
- Experimental work on the key biological control agents to determine their actual *per capita* impacts on *H. pilosella* reproduction or mortality rates.
- As part of post-release monitoring, determining likely densities in the field of the key control agent(s) in relation to both their own and *H. pilosella* density. Together with

the above, this will allow predictions of their likely ultimate impact when inserted into the *H. pilosella* model.

Acknowledgements

A special thank you to my supervisors, Dave Kelly and Nigel Barlow, for their support, encouragement and help throughout.

I wish to express my gratitude to AgResearch for funding, logistical support and access to their Mt. John trial site, to the Department of Plant and Microbial Sciences for additional funding and to Graeme Young for allowing me the use his Port Levy property for part of the field trials.

I would like to thank David Scott for helping to maintain the Mt. John trial, helping with field work, providing me with data and for sharing his knowledge of *H. pilosella*. I also wish to thank Alex Maunsell for help with plot maintenance at Mt John.

A big thank you to David Saville for user friendly guidance with experimental design and statistical analysis.

Thanks to Dave Kelly, Bronek Kazmierow, Nigel Barlow and especially Stan Van Uden and John Kean for the many hours they spent helping with field work and to Stan for taking hundreds of pictures and then sitting down and looking at them. Thank you also to Stan, Nigel and Dave for the many readings of thesis drafts.

I also wish to extend special thanks to two great friends: Ian Laurenson for never ending support on computer related issues and for providing well needed breaks from work and John Kean for hours of interesting conversations and distractions throughout the last three years. A huge thanks also to John for letting me “pirate” some of his programming code and for his time spent helping me to learn Turbo.

A warm thank you goes to my parents for their endless support and encouragement.

Finally, I wish to express a special thank you to Stan Van Uden for always believing in me and for his support, encouragement, commitment and companionship over the last several years.

This project was funded by The Foundation for Research, Science and Technology through a stipend from AgResearch.

References

- Allan, H.H. (1920) A note on weeds. *The Magazine of the Agricultural and Pastoral Association*, **1**, 39-40.
- Allan, H.H. (1940) A Handbook of the naturalised flora of New Zealand. *DSIR Research Bulletin*, **83**.
- Anonymous (1976) *Hieracium* - good or bad? *Tussock Grasslands and Mountain Lands Institute Review*, **32**, 48-54.
- Antonovics, J. & Levin, D.A. (1980) The ecological and genetic consequences of density-dependent regulation in plants. *Annual Review of Ecological Systems*, **11**, 411-452.
- Barker, A.P. (1953) An ecological study of tussock grassland; Hunters Hills, South Canterbury. *DSIR Research Bulletin*, **107**.
- Barkham, J.P. (1980) Population dynamics of the wild daffodil (*Narcissus pseudonarcissus*). I. Clonal growth, seed reproduction, mortality and the effects of density. *Journal of Ecology*, **68**, 607-633.
- Barkham, J.P. & Hance, C.E. (1982) Population dynamics of the wild daffodil (*Narcissus pseudonarcissus*). III. Implications of a computer model of 1000 years of population change. *Journal of Ecology*, **70**, 323-344.
- Barlow, N.D. (in press) Models in biological control: a field guide. *Theoretical Approaches to Biological Control* (Eds. B.A. Hawkins & H.B. Cornell), Cambridge University Press, Cambridge.
- Barlow, N.D. & Goldson, S.L. (1990) Modelling the impact of biological control agents. *Proceedings of the 43rd New Zealand Weed and Pest Control Conference* (Ed. A.J. Popay), pp. 282-283. Dunedin, New Zealand.
- Barlow, N.D. & Goldson, S.L. (1993) A modelling analysis of the successful biological control of *Sitona discoideus* (Coleoptera: Curculionidae) by *Microctonus aethiopiodes* (Hymenoptera: Braconidae) in New Zealand. *Journal of Applied Ecology*, **30**, 165-178.

- Baskin, J.M. & Baskin, C.M. (1979) Studies on the autecology and population biology of the weedy monocarpic perennial, *Pastinaca sativa*. *Journal of Ecology*, **67**, 601-610.
- Bellows, T.S. Jr. (1981) The descriptive properties of some models for density dependence. *Journal of Animal Ecology*, **50**, 139-156.
- Bishop, G.F. & Davy, A.J. (1984) Significance of rabbits for the population regulation of *Hieracium pilosella* in Breckland. *Journal of Ecology*, **72**, 273-284.
- Bishop, G.F. & Davy, A.J. (1985) Density and the commitment of apical meristems to clonal growth and reproduction in *Hieracium pilosella*. *Oecologia*, **66**, 417-422.
- Bishop, G.F. & Davy, A.J. (1994) Biological flora of the British Isles. *Hieracium pilosella* L. (*Pilosella officinarum* F. Schultz & Schultz-Bip.). *Journal of Ecology*, **82**, 195-210.
- Bishop, G.F., Davy, A.J. & Jefferies, R.L. (1978) Demography of *Hieracium pilosella* in a Breckland grassland. *Journal of Ecology*, **66**, 615-629.
- Cain, M.L. (1990) Models of clonal growth in *Solidago altissima*. *Journal of Ecology*, **78**, 27-46.
- Cain, M.L. & Cook, R.E. (1988) Growth in *Medeola virginiana* clones. II. Stochastic simulation of vegetative spread. *American Journal of Botany*, **75**, 730-736.
- Cain, M.L., Pacala, S.W. & Silander, J.A. Jr. (1991) Stochastic simulation of clonal growth in tall goldenrod, *Solidago altissima*. *Oecologia*, **88**, 477-485.
- Cain, M.L., Pacala, S.W., Silander, J.A. Jr. & Fortin, M.J. (1995) Neighborhood models of clonal growth in the white clover *Trifolium repens*. *American Naturalist*, **145**, 888-917.
- Callaghan, T.V., Svensson, B.M., Bowman, H., Lindley, D.K. & Carlsson, B.A. (1990) Model of clonal plant growth based on population dynamics and architecture. *Oikos*, **57**, 257-262.

- Carlsson, B.Å. & Callaghan, T.V. (1990) Effects of flowering on the shoot dynamics of *Carex bigelowii* along an altitudinal gradient in Swedish Lapland. *Journal of Ecology*, **78**, 152-165.
- Caswell, H. (1986) Life cycle models for plants. *Some Mathematical Questions in Biology - Plant Biology* (Eds. L.J. Gross & R.M. Miura), pp. 171-233. American Mathematical Society, Providence.
- Caswell, H. (1989) *Matrix Population Models*. Sinauer Associates Inc., Sunderland.
- Caswell, H. & Werner, P.A. (1978) Transient behavior and life history analysis of teasel (*Dipsacus sylvestris* Huds.). *Ecology*, **59**, 53-66.
- Cloutier, D. & Watson, A.K. (1989) Application of modelling to biological weed control. *Proceedings of the VII International Symposium on Biological Control of Weeds* (Ed. E.S. Delfosse), pp. 5-16. Istituto Sperimentale per la Patologia Vegetale, Rome, Italy.
- Comins, H.N., Hassell, M.P. & May, R.M. (1992) The spatial dynamics of host-parasitoid systems. *Journal of Animal Ecology*, **61**, 735-748.
- Comins, H.N. & Hassell, M.P. (1996) Persistence of multi-species host-parasitoid interactions in spatially distributed models with local dispersal. *Journal of Theoretical Biology*, **183**, 19-28.
- Connor, H.E. (1964) Tussock grassland communities in the Mackenzie Country, South Canterbury, New Zealand. *New Zealand Journal of Botany*, **2**, 325-351.
- Cossens, G.G. & Brash, D.W. (1980) Agronomic control of mouse-eared hawkweed (*Hieracium pilosella*). New Zealand MAF Annual Report 1978/79.
- Crawley, M.J. (1986) The structure of plant communities. *Plant Ecology* (Ed. M.J. Crawley), pp. 1-50. Blackwell Scientific, London.
- Crawley, M.J. & May, R.M. (1987) Population dynamics and plant community structure: competition between annuals and perennials. *Journal of Theoretical Biology*, **125**, 475-489.

- Czárán, T. (1998) *Spatiotemporal Models of Population and Community Dynamics*. Chapman and Hall, London.
- Czárán, T. & Bartha, S. (1989) The effect of spatial pattern on community dynamics; a comparison of simulated and field data. *Vegetatio*, **83**, 229-239.
- Davy, A.J. & Bishop, G.F. (1984) Response of *Hieracium pilosella* in Breckland grass-heath to inorganic nutrients. *Journal of Ecology*, **72**, 319-330.
- Deevey, E.S. (1947) Life tables for natural populations of animals. *Quarterly Review of Biology*, **22**, 283-314.
- DeGrandi-Hoffman, G., Diehl, J., Li, D., Flexner, L., Jackson, G., Jones, W. & Debolt, J. (1994) Biocontrol-Parasite: parasitoid-host and crop loss assessment simulation model. *Environmental Entomology*, **23**, 1045-1060.
- Enright, N. & Ogden, J. (1979) Applications of transition matrix models in forest dynamics: *Araucaria* in Papua New Guinea and *Nothofagus* in New Zealand. *Australian Journal of Ecology*, **4**, 3-23.
- Espie, P.R. (1994) Integrated pastoral management strategies for *Hieracium* control. *Proceedings of the New Zealand Grassland Association*, **56**, 243-247.
- Espie, P.R. & Boswell, C.C. (unpublished manuscript) *Hieracium pilosella* invasion in dry sub-humid and humid South Canterbury tussock grasslands. Submitted to *Journal of Ecology*, November 1997.
- Evans, H.C. & Ellison, C.A. (1990) Classical biological control of weeds with micro-organisms: past, present, prospects. *Aspects of Applied Biology*, **24**, 39-49.
- Fan, J. & Harris, W. (1996) Effects of soil fertility and cutting frequency on interference among *Hieracium pilosella*, *H. praealtum*, *Rumex acetosella* and *Festuca novae-zealandiae*. *New Zealand Journal of Agricultural Research*, **39**, 1-32.
- Fisher, R.A. (1937) The wave of advance of advantageous genes. *Annals of Eugenics*, **7**, 255-369.

- Foran, B.D., Bates, J., Murray, P., Heward, G. & Pickens, D. (1992) A paddock based survey of management factors relating to mouse-ear hawkweed (*Hieracium pilosella*) dominance in central Otago. *Vegetation Change in Tussock Grasslands, with Emphasis on Hawkweeds* (Eds. G.G. Hunter, C.R. Mason & D.M. Robertson), New Zealand Ecological Society Occasional Publication No. 2, pp. 64-68. New Zealand Ecological Society, Christchurch.
- Fornasari, L. (1996) Ecology of old world hawkweeds, *Hieracium* species (Asteraceae), in their homeland and consideration on their potential weediness. *Proceedings of the IX International Symposium on Biological Control of Weeds* (Eds. V.C. Moran & J.H. Hoffmann), pp. 11-18. University of Cape Town, Stellenbosch, South Africa.
- Genstat 5 Committee (1993) *Genstat 5 Release 3 Reference Manual*. Claredon Press, Oxford.
- Green, D.G. (1989) Simulated effects of fire, dispersal and spatial pattern on competition with forest mosaics. *Vegetatio*, **82**, 139-153.
- Gross, K.L. (1981) Predictions of fate from rosette size in four "biennial" plant species: *Verbascum thapsus*, *Oenothera biennis*, *Daucus carota*, and *Tragopogon dubius*. *Oecologia*, **48**, 209-213.
- Grundy, T.P. (1989) An Economic Evaluation of Biological Control of Hieracium. Agribusiness and Economics Research Unit, Lincoln College, Report No. 202.
- Hara, T. (1986) Effects of density and extinction coefficient on size variability in plant populations. *Annals of Botany*, **57**, 885-892.
- Hara, T. (1988) Dynamics of size structure in plant populations. *Trends in Ecology and Evolution*, **3**, 129-133.
- Hara, T. (1993) Effects of variation in individual growth on plant species coexistence. *Journal of Vegetation Science*, **4**, 409-416.
- Hara, T., Van der Toorn, J. & Mook, J.H. (1993) Growth dynamics and size structure of shoots of *Phragmites australis*, a clonal plant. *Journal of Ecology*, **81**, 47-60.

- Harper, J.L. (1977) *Population Biology of Plants*. Academic Press Inc., San Diego.
- Hartshorn, G.S. (1975) A matrix model of tree population dynamics. *Tropical Ecological Systems* (Eds. F.B. Golley & E. Medina), pp. 41-51. Springer-Verlag, New York.
- Hassell, M.P., Comins, H.N. & May, R.M. (1991) Spatial structure and chaos in insect population dynamics. *Nature*, **353**, 255-258.
- Hassell, M.P., Comins, H.N. & May, R.M. (1994) Species coexistence and self-organizing spatial dynamics. *Nature*, **370**, 290-292.
- Hay, J.R. & Ouellette, G.J. (1959) The role of fertilizer and 2,4-D in the control of pasture weeds. *Canadian Journal of Plant Science*, **39**, 278-283.
- Hendry, R.J., McGlade, J.M. & Weiner, J. (1996) A coupled map lattice model of the growth of plant monocultures. *Ecological Modelling*, **84**, 1-3, 81-90.
- Henn, G., Petit, D. & Vernet, P. (1988) Interference between *Hieracium pilosella* and *Arrhenatherum elatius* in colliery spoils of north of France. Allelopathy or competition? *Oecologia*, **76**, 268-272.
- Hirose, T. & Kachi, N. (1982) Critical plant size for flowering in biennials with special reference to their distribution in a sand dune system. *Oecologia*, **55**, 281-284.
- Hobbs, R.J. & Hobbs, V.F. (1987) Gophers and grassland: a model of vegetation response to patchy soil disturbance. *Vegetatio*, **69**, 141-146.
- Hoffmann, J.H. (1990) Interactions between three weevil species in the biocontrol of *Sesbania punicea* (Fabaceae): the role of simulation models in evaluation. *Agriculture, Ecosystems and Environment*, **32**, 77-87.
- Hughes, J.G. (1975) *A Study of the Grazing Preferences of Sheep on Developed and Undeveloped Grassland at a High-Country Site*. M.Agr.Sc. Thesis, Lincoln College, NZ.
- Hunter, G.G. (1991) The distribution of hawkweeds (*Hieracium* spp.) in the South Island, indicating problem status. *Journal of the New Zealand Mountain Lands Institute Review*, **48**, 21-31.

Hunter, G.G., Mason, C.R. & Robertson, D.M. (Eds.) (1992) *Vegetation Change in Tussock Grasslands, With Emphasis on Hawkweeds*. Occasional Publication No. 2. New Zealand Ecological Society, Christchurch.

Jenkins, T.A. (1992) A review of characteristics of mouse-ear hawkweed (*Hieracium pilosella*). *Vegetation Change in Tussock Grasslands, with Emphasis on Hawkweeds* (Eds. G.G. Hunter, C.R. Mason & D.M. Robertson), Occasional Publication No.2, pp. 15-23. New Zealand Ecological Society, Christchurch.

Jenkins, T.A. (1995) *Fungal Biological Control of Hieracium*. Ph.D. Thesis, University of Canterbury, NZ.

Kadmon, R. & Shmida, A. (1990) Spatiotemporal demographic processes in plant populations: an approach and a case study. *American Naturalist*, **135**, 382-397.

Kaneko, K. (1989) Spatiotemporal chaos in one- and two-dimensional coupled map lattices. *Physica D*, **37**, 60-82.

Kelly, D. (1985) On strict and facultative biennials. *Oecologia*, **67**, 292-294.

Kelly, D. (1989) Demography of short-lived plants in chalk grassland II. Control of mortality and fecundity. *Journal of Ecology*, **77**, 770-784.

Kerr, C.J. (1950) *The Pastoral Areas of the South Canterbury District. Pts. I and II*. South Canterbury Catchment Board, Timaru.

Klinkhamer, P.G.L., de Jong, T.J. & de Heidin, J.L.H. (1996) An eight-year study of population dynamics and life-history variation of the "biennial" *Carlina vulgaris*. *Oikos*, **75**, 259-268.

Lee, J.M. & Hamrick, J.L. (1983) Demography of two natural populations of musk thistle (*Carduus nutans*). *Journal of Ecology*, **71**, 923-936.

Lee, W.G., Fenner, M. & Duncan, R.P. (1993) Pattern of natural regeneration of narrow-leaved snow tussock *Chionochloa rigida* ssp. *rigida* in Central Otago, New Zealand. *New Zealand Journal of Botany*, **31**, 117-125.

- Leslie, P.H. (1945) On the use of matrices in certain population mathematics. *Biometrika*, **33**, 183-212.
- Leslie, P.H. (1948) Some further notes on the use of matrices in population mathematics. *Biometrika*, **35**, 213-245.
- Leslie, P.H. & Ransom, R.M. (1940) The mortality, fertility and rate of natural increase of the vole (*Microtus agrestis*) as observed in the laboratory. *Journal of Animal Ecology*, **9**, 27-52.
- Leverich, W.J. & Levin, D.A. (1979) Age-specific survivorship and reproduction in *Phlox drummondii*. *American Naturalist*, **113**, 881-903.
- Lloyd, P.S. & Pigott, C.D. (1967) The influence of soil conditions on the course of succession on the chalk of southern England. *Journal of Ecology*, **55**, 137-146.
- Lonsdale, W.M., Farrell, G. & Wilson, C.G. (1995) Biological control of a tropical weed: a population model and experiment for *Sida acuta*. *Journal of Applied Ecology*, **32**, 391-399.
- Lovett Doust, L. (1981) Population dynamics and local specialization in a clonal perennial (*Ranunculus repens*). I. The dynamics of ramets in contrasting habitats. *Journal of Ecology*, **69**, 743-755.
- MacDonald, N. & Watkinson, A.R. (1981) Models of an annual plant population with a seed bank. *Journal of Theoretical Biology*, **93**, 643-653.
- Mack, R.N. & Harper, J.L. (1977) Interference in dune annuals: spatial pattern and neighborhood effects. *Journal of Ecology*, **65**, 345-363.
- MAF (1992) Rabbit and Land Management News: Vegetation Monitoring 1991/92.
- MAF (1993) Rabbit and Land Management News: Vegetation Monitoring 1992/93.
- MAF (1994) Rabbit and Land Management News: Vegetation Monitoring 1993/94.
- MAF (1995) Rabbit and Land Management News: Vegetation Monitoring 1994/95.

- Makepeace, W. (1980) *Ecological Studies of Hieracium pilosella and H. praealtum*. Ph.D. Thesis, University of Canterbury, NZ.
- Makepeace, W. (1985a) Growth, reproduction, and production biology of mouse-ear and king devil hawkweed in eastern South Island, New Zealand. *New Zealand Journal of Botany*, **23**, 65-78.
- Makepeace, W. (1985b) Some establishment characteristics of mouse-ear and king devil hawkweeds. *New Zealand Journal of Botany*, **23**, 91-100.
- Makepeace, W., Dobson, A.T. & Scott, D. (1985) Interference phenomena due to mouse-ear and king devil hawkweed. *New Zealand Journal of Botany*, **23**, 79-90.
- May, R.M. (1973) On relationships among various types of population models. *American Naturalist*, **107**, 46-57.
- May, R.M., Hassell, M.P., Anderson, R.M. & Tonkyn, D.W. (1981) Density dependence in host-parasitoid models. *Journal of Animal Ecology*, **50**, 855-865.
- May, R.M. & Oster, G.F. (1976) Bifurcations and dynamic complexity in simple ecological models. *American Naturalist*, **110**, 573-599.
- McIntosh, P.D. & Allen, R.B. (1993) Soil pH declines and organic carbon increase under hawkweed (*Hieracium pilosella*). *New Zealand Journal of Ecology*, **17**, 59-60.
- McIntosh, P.D., Loeseke, M. & Bechler, K. (1995) Soil changes under mouse-ear hawkweed (*Hieracium pilosella*). *New Zealand Journal of Ecology*, **19**, 29-34.
- Meagher, T.R. (1982) The population biology of *Chamaelirium luteum*, a dioecious member of the lily family: two-sex population projections and stable population structure. *Ecology*, **63**, 1701-1711.
- Meagher, T.R. & Antonovics, J. (1982) The population biology of *Chamaelirium luteum*, a dioecious member of the lily family: life history studies. *Ecology*, **63**, 1690-1700.
- Moore, L.B. (1955) The plants of tussock grassland. *Proceedings of the New Zealand Ecological Society*, **3**, 7-8.

- Moore, L.B. (1976) The changing vegetation of Molesworth Station, New Zealand, 1944 to 1971. *DSIR Bulletin*, 217.
- Morin, L. & Syrett, P. (1996) Prospects for biological control of *Hieracium pilosella* with the rust *Puccinia hieracii* var. *piloselloidarum* in New Zealand. *Proceedings of the IX International Symposium on Biological Control of Weeds* (Eds. V.C. Moran & J.H. Hoffmann), pp. 199-204. University of Cape Town, Stellenbosch, South Africa.
- Nobel, P.S. (1987) Water relations and plant size aspects of flowering for *Agave deserti*. *Botanical Gazette*, 148, 79-84.
- Okubo, A. (1980) *Diffusion and Ecological Problems: Mathematical Models*. Springer-Verlag, New York.
- Pacala, S.W. (1986a) Neighborhood models of plant population dynamics. II. Multi-species models of annuals. *Theoretical Population Biology*, 29, 262-292.
- Pacala, S.W. (1986b) Neighborhood models of plant population dynamics. IV. Single-species and multispecies models of annuals with dormant seeds. *American Naturalist*, 128, 859-878.
- Pacala, S.W. (1987) Neighborhood models of plant population dynamics. III. Models with spatial heterogeneity in the physical environment. *Theoretical Population Biology*, 31, 359-392.
- Pacala, S.W. (1989) Plant Population Dynamic Theory. *Perspectives in Ecological Theory* (Eds. J. Roughgarden, R.M. May & S.A. Levin), pp. 54-67. Princeton University Press, Princeton, New Jersey.
- Pacala, S.W. & Silander, J.A. Jr. (1985) Neighborhood models of plant population dynamics. I. Single-species models of annuals. *American Naturalist*, 125, 385-411.
- Pacala, S.W. & Silander, J.A. Jr. (1990) Field tests of neighborhood population dynamic models of two annual weed species. *Ecological Monographs*, 60, 113-134.

- Pitelka, L.F. & Ashmun, J.W. (1986) The physiology and ecology of connections between ramets in clonal plants. *The Population Biology and Evolution of Clonal Organisms* (Eds. J.B.C. Jackson, L.W. Buss & R.E. Cook), Yale University Press, New Haven.
- Putwain, P.D., Machin, D. & Harper, J.L. (1968) Studies in the dynamics of plant populations. II. Components and regulation of a natural population of *Rumex acetosella* L. *Journal of Ecology*, **56**, 421-431.
- Qi, M., Upadhyaya, M.K. & Turkington, R. (1996) Reproductive behaviour of natural populations of meadow salsify (*Tragopogon pratensis*). *Weed Science*, **44**, 68-73.
- Rees, M. & Crawley, M.J. (1989) Growth, reproduction and population dynamics. *Functional Ecology*, **3**, 645-653.
- Rees, M. & Q. Paynter (1997) Biological control of scotch broom: modelling the determinants of abundance and the potential impact of introduced insect herbivores. *Journal of Applied Ecology*, **34**, 1203-1221.
- Rose, A.B., Platt, K.H. & Frampton, C.M. (1995) Vegetation change over 25 years in a New Zealand short-tussock grassland: effects of sheep grazing and exotic invasions. *New Zealand Journal of Ecology*, **19**, 163-174.
- Saltzman, A. (1985) Habitat selection in a clonal plant. *Science*, **228**, 603-604.
- Sarukhán, J. & Gadgil, M. (1974) Studies on plant demography: *Ranunculus repens* L., *R. bulbosus* L., and *R. acris* L. III. Mathematical model incorporating multiple modes of reproduction. *Journal of Ecology*, **62**, 921-936.
- Saville, D.J. & Wood, G.R. (1991) *Statistical Methods: The Geometric Approach*. Springer-Verlag, New York.
- Scott, D. (1975) Variation in soil pH under tussock grassland species. *New Zealand Journal of Experimental Agriculture*, **3**, 143-145.

- Scott, D. (1985) Hawkweeds in run country. *Tussock Grasslands and Mountain Lands Institute Review*, **42**, 33-48.
- Scott, D. (1993a) Response of *Hieracium* in two long term manipulative agricultural trials. *New Zealand Journal of Ecology*, **17**, 41-46.
- Scott, D. (1993b) Time segment analysis of permanent quadrat data: changes in *Hieracium* cover in the Waimakariri in 35 years. *New Zealand Journal of Ecology*, **17**, 53-57.
- Scott, D. & Covacevich, N. (1987) Effects of fertilizer and grazing on a pasture species mixture in high country. *Proceedings of the New Zealand Grassland Association*, **48**, 93-98.
- Scott, D., Robertson, J.S. & Archie, W.J. (1990a) Plant dynamics of New Zealand tussock grassland infested with *Hieracium pilosella*. I. Effects of seasonal grazing, fertiliser and overdrilling. *Journal of Applied Ecology*, **27**, 224-234.
- Scott, D., Robertson, J.S. & Archie, W.J. (1990b) Plant dynamics of New Zealand tussock grassland infested with *Hieracium pilosella* II. Transition matrices of vegetation change. *Journal of Applied Ecology*, **27**, 235-241.
- Scott, D. & Sutherland, B.L. (1993) Interaction between some pasture species and two *Hieracium* species. *New Zealand Journal of Ecology*, **17**, 47-51.
- Shea, K. (1994) *Matrix Models in Population Ecology*. Ph.D. Thesis, University of London, UK.
- Shea, K. & Kelly, D. (in press) Estimating biocontrol agent impact with matrix models: *Carduus nutans* in New Zealand. *Ecological Applications*.
- Shigesada, N. & Kawasaki, K. (1997) *Biological Invasions: Theory and Practice*. Oxford University Press, New York.
- Silvertown, J. (1987) *Introduction to Plant Population Ecology*, 2 ed. Longman Scientific and Technical, Essex.

- Silvertown, J. (1991) Modularity, reproductive thresholds and plant population dynamics. *Functional Ecology*, **5**, 577-580.
- Skellam, J.G. (1951) Random dispersal in theoretical populations. *Biometrika*, **38**, 196-218.
- Slade, A.J. & Hutchings, M.J. (1987) An analysis of the influence of clone size and stolon connections between ramets on the growth of *Glechoma hederacea* L. *New Phytologist*, **106**, 759-771.
- Smith, M.C., Holt, J. & Webb, M. (1993) Population model of the parasitic weed *Striga hermonthica* (Scrophulariaceae) to investigate the potential of *Smicronyx umbrinus* (Coleoptera: Curculionidae) for biological control in Mali. *Crop Protection*, **12**, 470-476.
- Snedecor, G.W. & Cochran, W.G. (1980) *Statistical Methods*, 7 ed. The Iowa State University Press, Ames.
- Stevens, E.J. & Hughes, J.G. (1973) Distribution of sweet briar, broom and ragwort on Molesworth Station. *Tussock Grassland and Mountain Lands Institute Special Publication 9*.
- Svavarsdóttir, K. (1995) *Effects of Added Nutrients on Species Composition in Native Tussock Grasslands*. Ph.D. Thesis, Lincoln University, NZ.
- Syrett, P., Harman, H.M., Grosskopf, G. & Smith, L.A. (1996) Insects for biological control of hieracium in New Zealand: a progress report. *Proceedings of the IX International Symposium on Biological Control of Weeds* (Eds. V.C. Moran & J.H. Hoffmann), pp. 213-218. University of Cape Town, Stellenbosch, South Africa.
- Syrett, P. & Sároszpataki, M. (1993) Prospects for biological control of hawkweeds with insects. *Proceedings of the 6th Australasian Grassland Invertebrate Ecology Conference* (Ed. R.A. Prestidge), pp. 426-432. AgResearch, Hamilton, New Zealand.
- Thomas, A.G. & Dale, H.M. (1974) Zonation and regulation of old pasture populations of *Hieracium floribundum*. *Canadian Journal of Botany*, **52**, 1451-1458.

- Thompson, D.A. & Beattie, A.J. (1981) Density-mediated seed and stolon production in *Viola* (Violaceae). *American Journal of Botany*, **68**, 383-388.
- Tilman, D. (1994) Competition and biodiversity in spatially structured habitats. *Ecology*, **75**, 2-16.
- Treskonova, M. (1991a) Changes in the structure of tall tussock grasslands and infestation by species of *Hieracium* in the Mackenzie Country, New Zealand. *New Zealand Journal of Ecology*, **15**, 65-78.
- Treskonova, M. (1991b) Hieracium - an ecological perspective. *Journal of the NZ Mountain Lands Institute Review*, **48**, 32-40.
- Turkington, R. & Harper, J.L. (1979) The growth, distribution, and neighbour relationships of *Trifolium repens* in permanent pasture (I-IV). *Journal of Ecology*, **67**, 201-254.
- Usher, M.B. (1966) A matrix approach to the management of renewable resources, with special reference to selection forests. *Journal of Applied Ecology*, **3**, 355-367.
- Usher, M.B. (1969a) A matrix approach to the management of renewable resources, with special reference to selection forests-two extensions. *Journal of Applied Ecology*, **6**, 347-348.
- Usher, M.B. (1969b) A matrix model for forest management. *Biometrics*, **25**, 309-315.
- van der Meijden, E. & van der Waals-Kooi, R.E. (1979) The population ecology of *Senecio jacobaea* in a sand dune system. I. Reproductive strategy and the biennial habit. *Journal of Ecology*, **67**, 131-153.
- van Tongeren, O. & Prentice, I.C. (1986) A spatial simulation model for vegetation dynamics. *Vegetatio*, **65**, 163-173.
- Waller, D.M. (1988) Plant morphology and reproduction. *Plant Reproductive Ecology: Patterns and Strategies* (Eds. J. Lovett Doust & L. Lovett Doust), pp. 203-227. Oxford University Press, New York.

- Wang, Y.H. & Gutierrez, A.P. (1980) An assessment of the use of stability analyses in population ecology. *Journal of Animal Ecology*, **49**, 435-452.
- Watkinson, A.R. (1980) Density-dependence in single-species population of plants. *Journal of Theoretical Biology*, **83**, 345-357.
- Watt, A.S. (1962) The effect of excluding rabbits from grassland A (Xerobrometum) in Breckland, 1936-60. *Journal of Ecology*, **50**, 181-198.
- Watt, A.S. (1981) Further observations on the effects of excluding rabbits from grassland A, in East Anglia Breckland: the pattern of change and factors affecting it (1936-37). *Journal of Ecology*, **69**, 509-536.
- Webb, C.J., Sykes, W.R. & Garnock-Jones, P.J. (1988) *Flora of New Zealand. Volume 4. Naturalised Pteridophytes, Gymnosperms, Dicotyledons*. Botany Division, DSIR, Christchurch.
- Weiner, J. (1982). A neighborhood model of annual-plant interference. *Ecology*, **63**, 1237-1241.
- Weiner, J. (1988) The influence of competition on plant reproduction. *Plant Reproductive Ecology: Patterns and Strategies* (Eds. J. Lovett Doust & L. Lovett Doust), pp. 228-245. Oxford University Press, New York.
- Weiner, J. & Conte, P.T. (1981) Dispersal and neighborhood effects in an annual plant competition model. *Ecological Modelling*, **13**, 131-147.
- Werner, P.A. (1975) Predictions of fate from rosette size in teasel (*Dipsacus fullonum* L.). *Oecologia*, **20**, 197-201.
- Werner, P.A. & Caswell, H. (1977) Population growth rates and age versus stage-distribution models for teasel (*Dipsacus sylvestris* Huds.). *Ecology*, **58**, 1103-1111.
- Widera, M. (1978) Competition between *Hieracium pilosella* L. and *Festuca rubra* L. under natural conditions. *Ekologia Polska*, **26**, 359-390.

Wijesinghe, D.K. & Hutchings, M.J. (1997) The effects of spatial scale of environmental heterogeneity on the growth of a clonal plant: an experimental study with *Glechoma hederaces*. *Journal of Ecology*, **85**, 17-28.

Wolfram, S. (1984) Cellular automata as models of complexity. *Nature*, **311**, 419-424.

Zar, J.H. (1996) *Biostatistical Analysis*, 3rd ed. Prentice Hall, New Jersey.

